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AN ANALYSIS OF POPULATIONS FORMED BY HYBRIDIZATION BETWEEN PHYLLODOCE EMPETRIFORMIS AND P. GLANDULIFLORA (ERICACEAE)

THOMAS J. WATSON, JR.

Phyllodoce is a genus of seven or eight arctic-alpine subshrubs that are distributed primarily in Asia and North America. Two of the species, *P. empetriformis* (J. E. Smith) D. Don and *P. glanduliflora* (W. J. Hooker) Coville, range in the mountains from Alaska to northern California and Wyoming (Figure 1). Over this region *P. glanduliflora* grows in alpine habitats (usually above 1950 m elevation) which are subject to full insolation and seasonally severe fluctuations in temperature and soil moisture. Populations of *P. empetriformis* are more commonly found at lower elevations (ca. 1500–2000 m) in scattered subalpine forests where climatic conditions are milder. At many sites, however, the distribution of the latter extends into the alpine-subalpine ecotone. Here the two species of *Phyllodoce* grow intermixed and hybridization often occurs. From the intermixed populations an F_1 hybrid — *P.* × *intermedia* (Hook.) Rydb. — was described in 1834 by Hooker (as *Menziesia intermedia* Hook.). Later, Rydberg (1900) recognized a backcross to *P. glanduliflora* as *P. hybrida* Rydb. Camp (1939) observed that the hybridizing populations were morphologically complex "hybrid swarms" and stated that "they [the hybrids] are so numerous and variable that I feel it would be an unnecessary burden upon taxonomic literature to attempt definitive descriptions of the many variants of which I have knowledge." Although precise measurements were not attempted, the formal descriptions and Camp's subsequent evaluation imply that the hybrid populations are typical Andersonian "hybrid swarms"

(Anderson, 1949) with relatively large numbers of F_1s, subsequent filial generations, and backcrosses to both parental species. After examination of herbarium material from the northwestern United States and cursory investigation of a single hybridizing stand at Trapper Peak in Montana, my impressions were that the "swarms" were of simple constitution. The preliminary data suggested that the populations consisted largely of F_1s with very rare advanced filial and/or backcross generations. This investigation was initiated to provide a more accurate account of population structure and gene flow in the hybrid stands.

MATERIALS AND METHODS

For purposes of analysis, 14 populations were sampled (Table 1). Ten of these were either populations of single species or intermixed stands of both species in which no hybrids could be found. Four populations contained both hybrids and parents. A total of 288 plants was examined of which 197 were from hybridizing stands. In addition, specimens from several herbaria (see ACKNOWLEDGMENTS) in the United States and Canada were inspected.

Each individual from a sample was measured for five floral characteristics (Table 2). From these data pictorialized scatter diagrams were prepared (Figures 2, 5, & 6). All measurements were made on dried, pressed materials. The voucher specimens are on deposit in MONTU.

Each plant was examined for flavonoid constituents. The chromatographic and analytical techniques were in general those employed by Harborne (1967) and by Mabry, *et al.* (1970). The flowers and leaves of each plant were extracted separately for 24 hours in 85% aqueous methanol. Extracts of each organ were developed two dimensionally on Whatmann 3MM paper using tertiary butyl alcohol: acetic acid: water (3:1:1 v/v/v) and 15% aqueous acetic acid respectively.

The flavonoids were isolated for further analysis by eluting each compound obtained as a spot on paper with spectral methanol. Each compound was partially characterized by ultraviolet spectral analyses in diagnostic reagents and subsequently hydrolyzed for one hour in 2N HCl to remove the sugars. The aglycone was extracted from the hydrolysis mixture with ethyl acetate, subjected to ultraviolet spectral analysis, and co-chromatogrammed

Figure 1. Distribution of two species of *Phyllodoce*. Stippled area, *P. empetriformis;* diagonal lines, *P. glanduliflora.*

Table 1. **Populations Sampled**[1]

Montana

RAVALLI CO.; Bitterroot Mtns., Bitterroot Natl. Forest:
Twin Lakes, ca. 2100 m, 30 June 1973, *Watson 951* (8 plants).
*Trapper Peak, 2820 m, 12 July 1973, *Watson 958* (28 plants).
St. Mary's Peak, 2800 m, 7 July 1973, *Schaack 862* (19 plants).
DEERLODGE CO.; Anaconda-Pintlar Mtns., Deerlodge Natl. Forest:
*Storm Lake, 2490 m, 19 July 1973, *Watson 976* (49 plants).
Goat Flat, 2790 m, 19 July 1973, *Watson 982* (10 plants).
MISSOULA CO.; Lolo Natl. Forest:
Squaw Peak, 2399 m, 26 July 1970, *Watson 990* (14 plants).

Idaho

IDAHO CO.: Papoose Saddle, Bitterroot Mtns., Clearwater Natl. Forest, ca. 1900 m, 28 July 1973, *Watson 994* (5 plants).
Orogrande Summit, Clearwater Mtns., Nezperce Natl. Forest, ca. 1950 m, 28 July 1973, *Watson 996* (6 plants).
SHOSHONE CO.: Freezeout Saddle, Clearwater Mtns., St. Joe Natl. Forest, 1800 m, 2 August 1973, *Watson 997* (8 plants).

Wyoming

PARK CO.: *Beartooth Pass, Beartooth Mtns., Shoshone Natl. Forest, 3280 m, 4 August 1973, *Watson 1000* (66 plants).

Alberta: *Highwood Pass, Rocky Mtns. Forest, 2180 m, 19 August, 1973, *Watson 1009* (54 plants).
Sunwapta Pass, Banff Natl. Park, 2160 m, 21 August 1973, *Watson 1017* (4 plants).
Bow Pass, Crowsnest Forest, 2010 m, 21 August 1973, *Watson 1016* (12 plants).

British Columbia: Mt. Apex, Manning Provincial Park, 2100 m, 2 September 1973, *Watson 1052* (5 plants).

[1]The number of plants collected at each site appears in parentheses.
*Hybridizing populations.

with authentic compounds on paper using the solvent systems described above.

Plants from each site were measured for pollen viability by staining on a microscope slide in aceto-carmine. Grains with normally symmetrical walls, well-developed cytoplasm, and darkly staining nuclei were scored as viable. Percentage of viability was based on random counts of 500 grains from anthers of one to three flowers per plant.

Chromosome studies were attempted but were largely unsuccessful due, perhaps, to the harsh fixative (modified Carnoy's solution) utilized. A count of $2n = 24$ was obtained from a single individual of *Phyllodoce empetriformis*. One count has been previously reported for *P. glanduliflora* as $2n = 24$ (Taylor & Mulligan, 1968).

OBSERVATIONS AND RESULTS

Morphology. *Phyllodoce empetriformis* and *P. glanduliflora* are relatively uniform species in morphological attributes. Vegetatively the two are virtually indistinguishable. Both are woody subshrubs from 10 to 20 cm in height at alpine elevations (*P. empetriformis* is larger at lower altitudes). In alpine regions, the two species are rhizomatous and form clumps 3 to 15 dm in diameter. Both have glabrate, linear leaves with serrulate margins and an abaxial furrow.

The two species differ markedly in flower structure (Figures 2 & 3). The corolla of *Phyllodoce empetriformis* is campanulate and deep pink to violet. The corolla mouth is open and 4.5–8.0 mm in diameter. The style is long and the stigma is greatly exserted. The sepals are short with obtuse apices. The perianth is glabrous.

Phyllodoce glanduliflora has a dirty yellow to yellow-green, urceolate corolla with a narrow mouth. The style is short and the stigma is included. The sepals are long with acute apices. The perianth is moderately to densely pubescent with glandular hairs.

Plants with intermediate morphology or with recombinations of the above floral characters were found only in sites where the two species grow intermixed. The plants recognized as F_1 hybrids in this study (see DISCUSSION) are enclosed by dotted lines on the scatter diagrams (Figures 5 & 6). These progeny are intermediate in every aspect of floral morphology (Figure 3). They have a near campanulate corolla with a slightly constricted mouth; the corolla is cream pink in coloration. The perianth is sparsely glandular. The sepals are of intermediate length and shape. The styles are of intermediate length. The stigma is only slightly exserted.

Filials subsequent to the F_1 exhibited combinations of quantitative and/or qualitative features found in neither the F_1s nor the parental species. These are designated as A1–A8 in Figures 5 and 6. The backcrosses were morphologically intermediate between the F_1 and recurrent species or closely resembled the recurrent

Table 2. **Floral Features and Symbols for Scatter Diagrams**

Character	P. glanduliflora	Intermediate	P. empetriformis
Style length	1.2-3.5 mm	3.6-4.4 mm	4.5 mm or more
Diameter of corolla mouth	1.0-2.5 mm	2.6-4.4 mm	4.5 mm or more
Perianth pubescence	± densely glandular 	sparsely glandular 	glabrous 
Sepal length	3.5 mm or more 	2.9-3.4 mm 	2.8 mm or less 
Corolla color	yellowish 	cream pink 	deep pink-violet 

parent while retaining features found in the noncurrent species. The backcrosses are designated as B1–B16 in Figures 5 and 6.

Flowering Periods. Flowering in *Phyllodoce glanduliflora* is initiated about the third week in June shortly after the snow melts. The populations reach peak anthesis in mid-July and continue flowering until mid-August. In alpine habitats, *P. empetriformis* begins to flower about one week after *P. glanduliflora* and reaches a zenith in middle to late July, ending in late August. The hybrids commence flowering simultaneously with *P. glanduliflora* in June and continue to do so until mid-August. Thus in July and August there is a broad overlap in which there are numerous mature plants of both parents and hybrids in the areas of sympatry available for pollination.

Pollen Viability. Pollen viability measured from individuals of *Phyllodoce empetriformis* was high, ranging largely from 80 to 100% good pollen (mean pollen viability = 91%; standard deviation = 9.9). Individuals of *P. glanduliflora* likewise produced a high percentage of viable grains (range = 75–99%; mean viability = 90%; standard deviation = 9.9).

Plants recognized here as F_1 hybrids exhibited a broad range of pollen viability (0–52%), having a mean of 35% which is considerably lower than the norm of the parental species. Filial generations subsequent to the F_1 ranged from 6 to 48% good grains. Backcrosses produced 46 to 85% viable pollen.

Flavonoid Chemistry. The two species produce a total of ten major flavonoid constituents representing three molecular classes: flavonols, anthocyanins, and dihydroflavonols (Figure 4). The aglycone and position of sugar attachment of some compounds have been determined. Others have not yet been identified or are identified only to molecular class.

Phyllodoce glanduliflora produces flavonoids 6–10 in both flowers and leaves (Figure 4). *Phyllodoce empetriformis* and the F_1 progeny synthesize all ten molecules in the flowers but only compounds 4–10 are found in the leaves. Also, each individual in a pure or nonhybridizing population produces every major compound listed for the profile of that species. Variation was noted only in the quantitative expression of the major flavonoids and in the sporadic occurrence of minor (i.e., weakly visible) constituents. Recombination of major flavonoids was noted only in some advanced filial segregates and in backcrosses to *P. glanduliflora*.

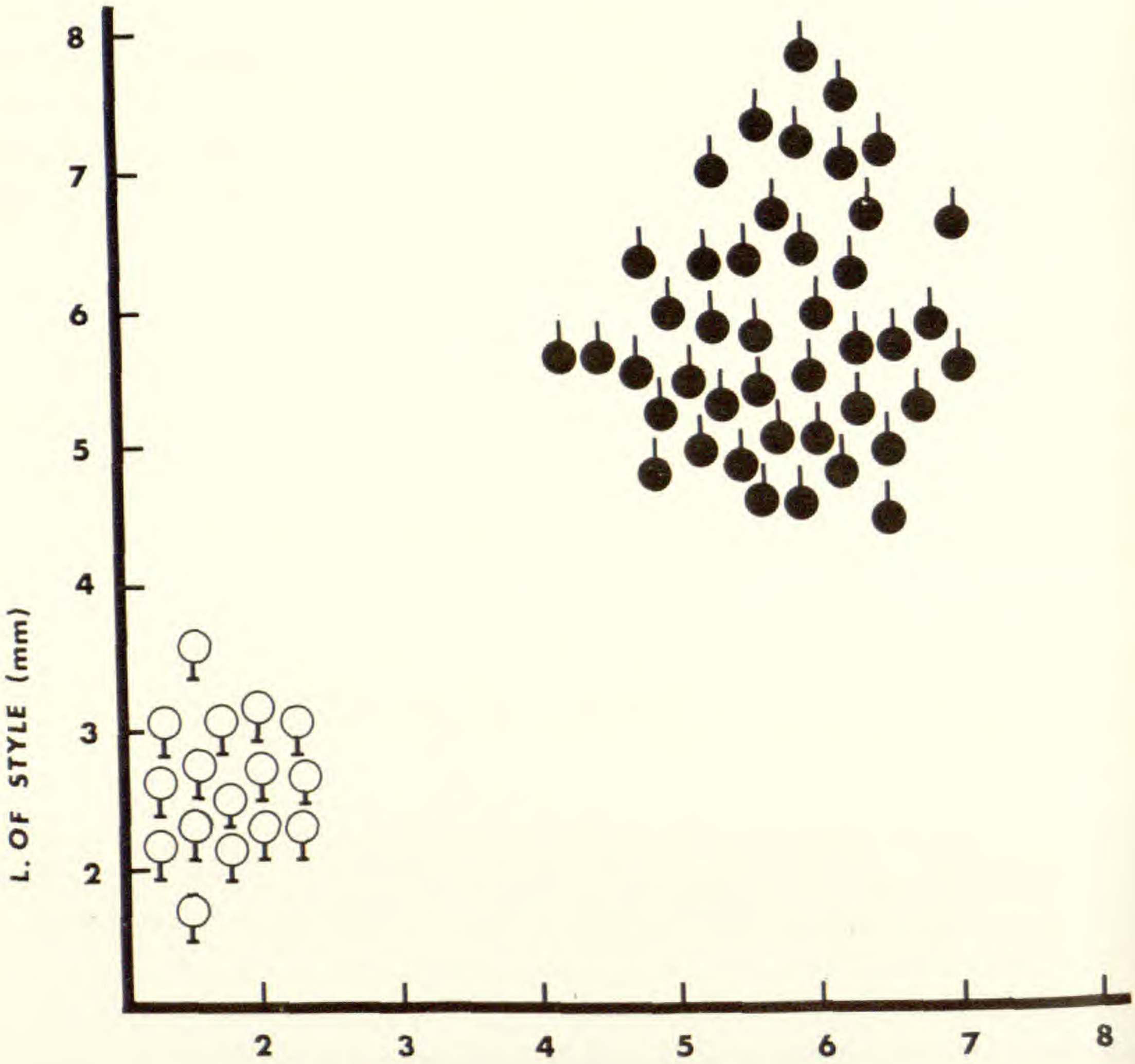

Figure 2. Representative scatter diagram of plants from uncontaminated populations of *Phyllodoce empetriformis* and *P. glanduliflora*. Symbols are listed in Table 2.

In the species of *Phyllodoce* investigated, there appear to be at least two independently segregating linkage groups among the flavonoids: the anthocyanins (spots 1–3) are block-inherited and spots 4 and 5 cohere. Similar linkages are known in flavonoids of *Tragopogon* (Belzer & Ownbey, 1971). While the *Phyllodoce* parents are seemingly homozygous for the loci controlling qualitative expression of these flavonoids, the F_1 is likely heterozygous since neither the anthocyanins nor spots 4 and 5 are produced in *P. glanduliflora*. Recombination of the constituents of each block was not observed in filial generations subsequent to

the F_1 nor in backcrosses. However, four advanced filial segregates and one putative backcross produced the anthocyanins but lacked spots 4 and 5. One backcross synthesized spots 4 and 5 but not the anthocyanins.

DISCUSSION

Flavonoids of *Baptisia* (Turner & Alston, 1959; Alston & Turner, 1962, 1963; McHale & Alston, 1964), *Phlox* (Levin, 1967), *Heterocentron* (Whiffen, 1973), and others have been useful in determining the structure of hybrid populations. In these instances, the parental species had significantly different flavonoid profiles. Each taxon possessed a number of diagnostic compounds that were additive in F_1 progeny and were recombined in some advanced filial segregates and in some backcrosses. In the present study, flavonoid chemistry was of limited value in analyzing the hybrid stands due to the similarity of the parental profiles and to the manner of flavonoid inheritance.

F_1 hybridity in *Phyllodoce* could not be documented on a purely chemical basis because there are no unique molecules contributed to hybrid zygotes by *P. glanduliflora*. The F_1s were identified as having intermediate exomorphic features and low pollen viability. Plants of this generation synthesized all ten flavonoids as expected. Thirty-three individuals were tentatively identified as F_1 progeny (Figures 5 & 6). Probably, a few plants interpreted here as F_1s are actually advanced filial segregates that resemble the F_1 (cf. Anderson, 1949). This probability might account for the broad range of pollen viability observed in the F_1 generation (see RESULTS).

Advanced filial segregates exhibit combinations of morphological characteristics found in neither F_1s nor parents (Figures 5 & 6). Additionally, four plants (A1, A3, A4 and A8 in Figures 5 & 6) have recombinations of flavonoids: the four synthesize the anthocyanins but lack spots 4 and 5. The remaining filial derivatives (A2, A5, A6 and A7 in Figures 5 & 6) elaborate all ten flavonoids. Advanced filials appear to occur infrequently in the hybrid stands. Only eight individuals of this type were found.

Phyllodoce glanduliflora produces no biochemical markers by which to detect backcrossing to *P. empetriformis*. Backcrosses to the latter were recognized by having features of the non-recurrent parent and intermediate pollen viability. All individuals identifield as backcrosses in this direction elaborate the ten flavonoids

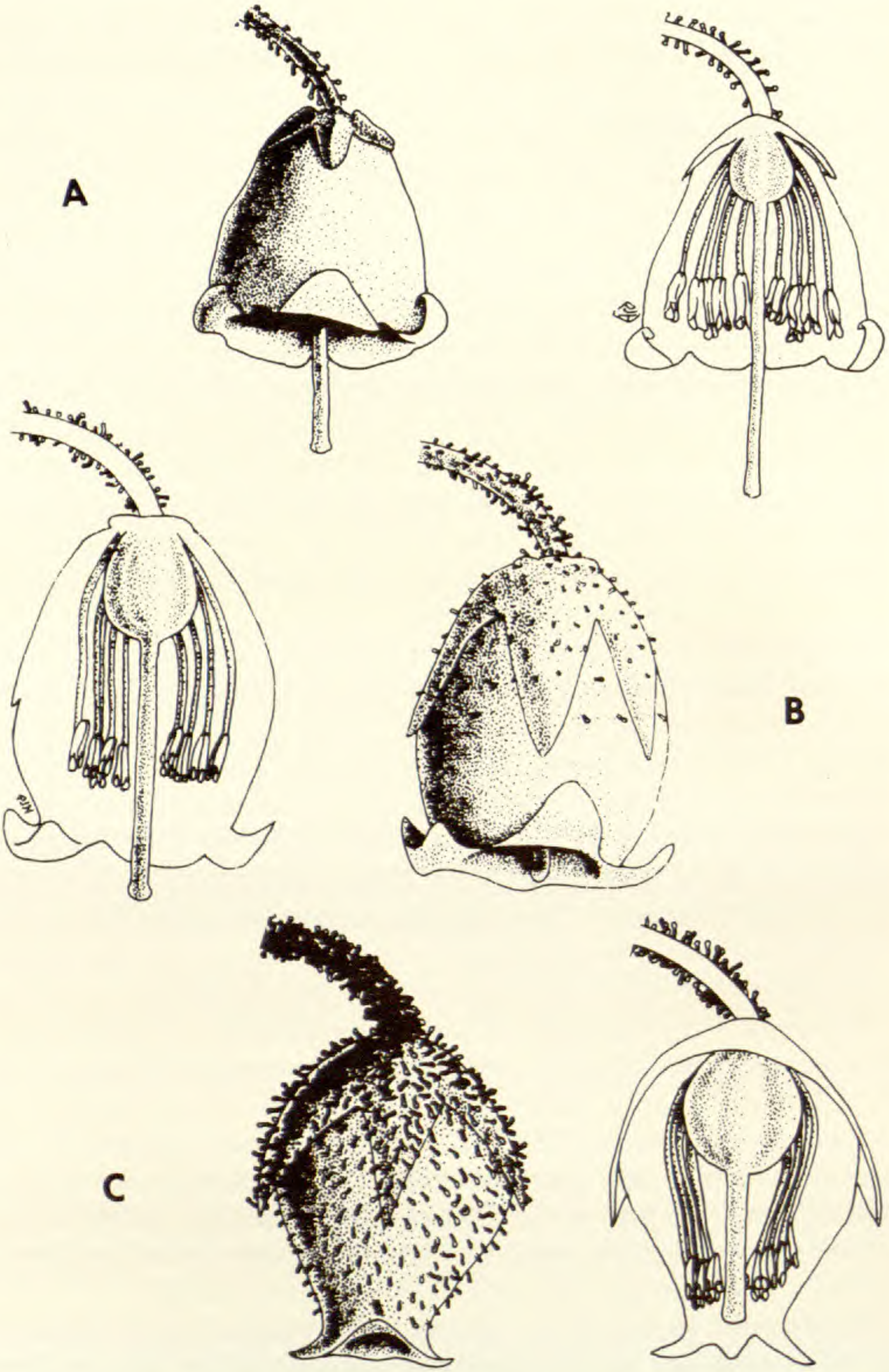

Figure 3. Flowers of *Phyllodoce*. A, *P. empetriformis*; B, F_1 hybrid (*P.* × *intermedia*); C, *P. glanduliflora*.

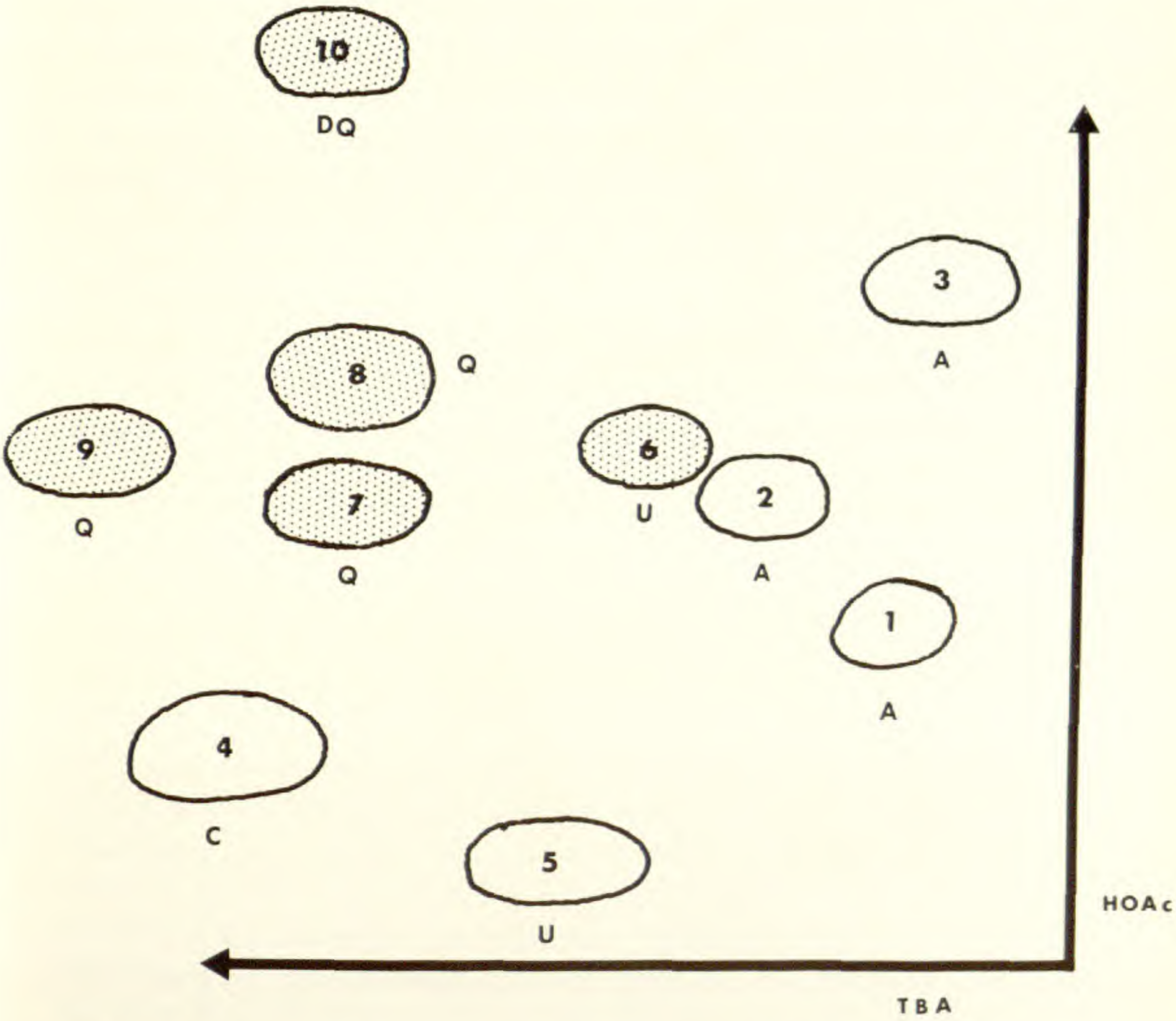

Figure 4. Composite two-dimensional chromatogram of flavonoids in leaves and flowers of *Phyllodoce empetriformis* and *P. glanduliflora*. The stippled spots are synthesized by both species; the remaining compounds are found in *P. empetriformis*. A = anthocyanins; C = caryatin; DQ = dihydroquercetin glycoside; Q = quercetin 3-0-glycosides; U = unknown.

of the recurrent parent. The majority of the backcrosses to *P. empetriformis* fall well within the limits of the taxon in most morphological aspects but have traits attributable to infiltration of genes from *P. glanduliflora* (see B2, B3, B7, B8, B9, B10, B11 and B12 in Figures 5 & 6). These individuals closely resemble the *P. empetriformis* parent but have longer sepals and a few glandular hairs on the perianth. Pollen viability of these plants ranged from 60 to 82%, which is slightly lower than the norm for parental plants. These data are consistent with the interpretation that the

plants are introgressants. Five of the latter (B2, B3, B7, B11 and B12 in Figures 5 & 6) have corollas with hues of pink that are intermediate between the pale pink of the F_1s and the deep pink of the recurrent parent, suggesting segregation of genes which regulate the quantity of anthocyanins produced. Other plants tentatively identified as backcrosses (B4, B5, B6, B13 and B14 in Figure 6) are morphologically intermediate to the F_1 and *P. empetriformis*. Pollen viability for the five plants ranged from 46 to 65% viable pollen. These data suggest that the plants are first generation backcrosses but do not preclude F_1 or subsequent filial hybridity. In this survey, at least eight backcrosses to *P. empetriformis* were recovered.

There were few independently segregating flavonoid markers by which to measure gene flow from *Phyllodoce empetriformis* into *P. glanduliflora*. However, extensive backcrossing to the latter should provide numerous plants resembling *P. glanduliflora* but having flavonoid profiles with one or both *P. empetriformis* linkage groups (i.e., anthocyanins and/or spots 4 and 5) and/or *P. empetriformis* morphological traits. Few plants of this type were recovered. Rather, backcrossing to *P. glanduliflora* seems to occur rarely. Only three plants in the samples may represent backcrosses to the latter taxon (i.e., B1, B15 and B16 in Figures 5 & 6). Two individuals (B1 and B15) are morphologically intermediate between the F_1 and *P. glanduliflora*. B1 produces the anthocyanins but not spots 4 and 5; whereas B15 elaborates all flavonoids. Pollen viability of the plants was 62% and 65% respectively. Although these plants are tentatively identified as backcrosses, they may in fact be filials.

A single individual, B16, was confirmed as a backcross to *Phyllodoce glanduliflora*. This plant resembles *P. glanduliflora* in all morphological aspects but synthesizes the *P. empetriformis* marker compounds 4 and 5. The plant had 85% viable pollen.

The populations created by hybridization between *Phyllodoce empetriformis* and *P. glanduliflora* are apparently simpler than might have been thought previously. Of 197 plants examined from sites of hybridization, 56 appear to be hybrids and their derivatives. The most complex stands are composed largely of parental species and F_1 progeny with relatively small numbers of advanced filial segregates and backcrosses. Backcrossing, when occurring, is largely to *P. empetriformis*. Backcrossing to *P. glanduliflora*

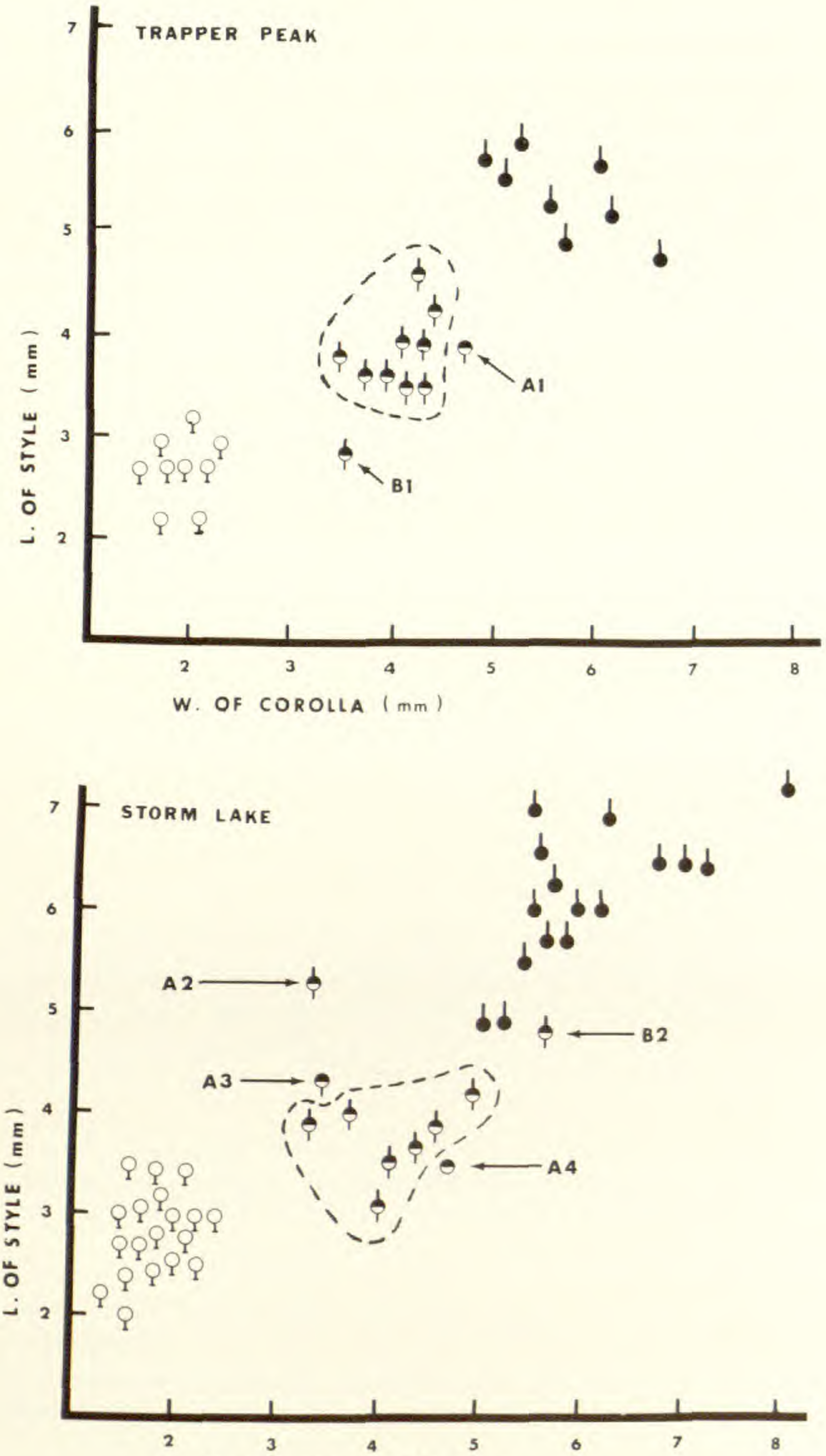

Figure 5. Pictorialized scatter diagrams of variation measured in the Trapper Peak and Storm Lake hybrid populations. Symbols are listed in Table 2. Trapper Peak = *Watson 958* (Table 1); Storm Lake = *Watson 976* (Table 1). Putative F_1 progeny are enclosed within broken lines. Filial segregates are designated as A1–A4. Backcrosses are designated as B1 and B2.

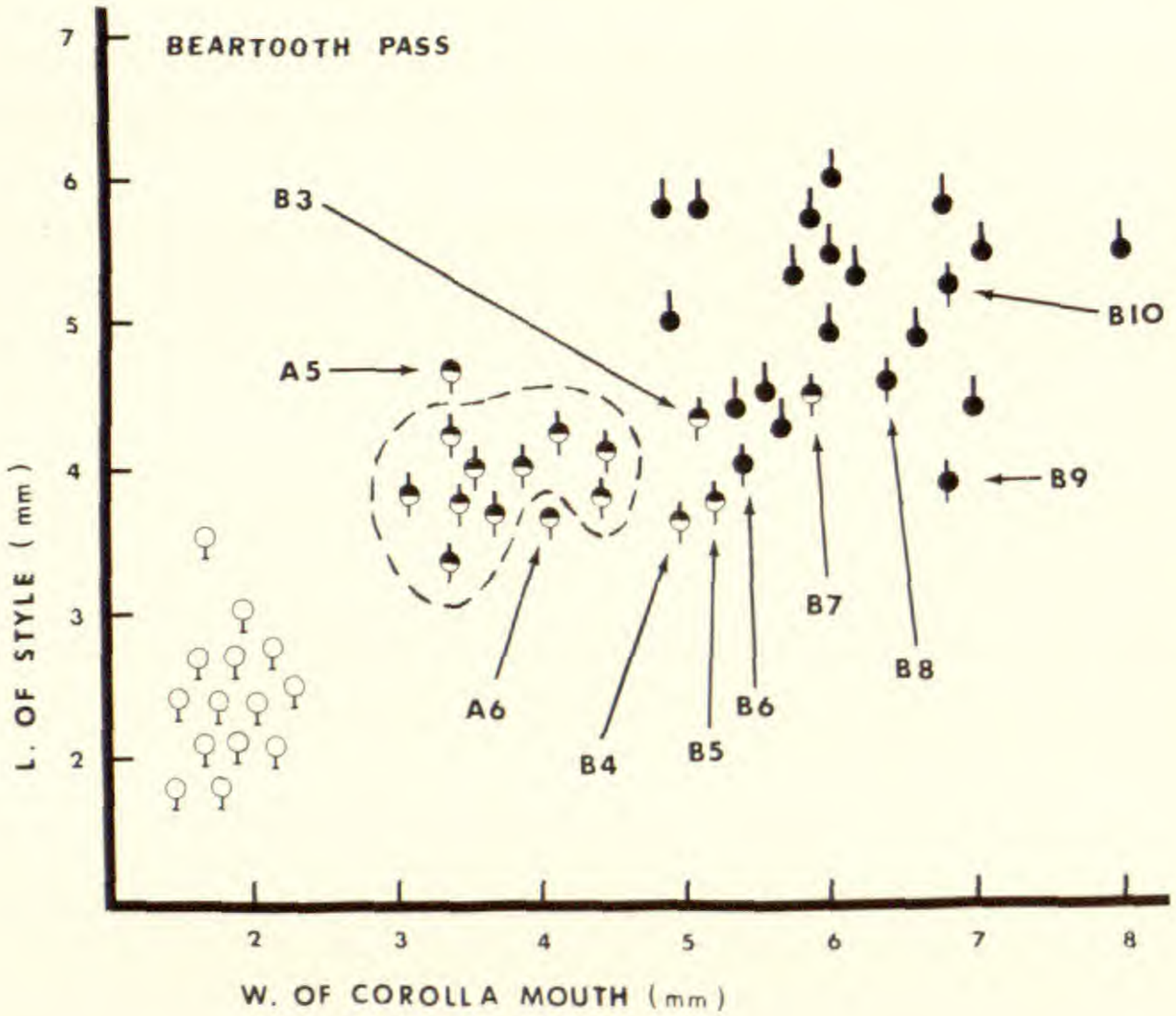

Figure 6. Pictorialized scatter diagrams representative of variation measured in the Beartooth Pass and Highwood Pass hybrid populations. Symbols are listed in Table 2. Beartooth Pass = *Watson 1000* (Table 1); Highwood Pass = *Watson 1009* (Table 1). Putative F_1 progeny are enclosed within broken lines. Filial segregates are designated as A5 – A8. Backcrosses are designated as B3 – B16.

is a rare event. The small amount of gene exchange between the species is restricted to the narrow zones where the two grow intermixed.

While only four sites of hybridization were examined intensively in this investigation, similar population structures probably exist at other locales. This is suggested by herbarium studies in which specimens from 31 other sites of hybridization throughout the range of the taxa were examined. A few of these appeared to be advanced filials or backcrosses to *Phyllodoce empetriformis.* Most seemed to be pure parents or F_1 hybrids. Only two specimens from 1,538 sheets examined were suspected of being backcrosses to *P. glanduliflora.* These were Rydberg's types of *P. hybrida* (*Rydberg & Bessey, 4657:* US, NY).

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DEPARTMENT OF BOTANY
THE UNIVERSITY OF MONTANA
MISSOULA, MONTANA 59801

A SUMMARY OF EXPERIMENTAL HYBRIDIZATION IN VERBESINA (COMPOSITAE)[1]

JAMES R. COLEMAN

Verbesina, a genus of approximately 250 species, ranges from southern Canada into Argentina and has its greatest concentration of species in Mexico and Central America. During the past decade, I have published papers on the experimental hybridization of the United States species (Coleman, 1968, 1971, 1974). The object of this paper is to present information on previously unreported experimental F_1 hybrids and to synthesize and summarize the results of the experimental hybridization program.

The cytological methods employed are essentially those given in the previously cited papers. Collection sites for the parent plants used in the production of the newly reported F_1s are as follow: *Verbesina alternifolia* (L.) Britton ex Kearney, Clarke Co., Ga., Izard Co., Ark., and Montgomery Co., Md.; *V. aristata* (Ell.) A. A. Heller, Holmes Co., Fla.; *V. glabrata* H. & A., São Paulo, Brazil; *V. helianthoides* Michx., Sumter Co., Ala.; *V. heterophylla* (Chapman) A. Gray, Baker Co., Fla.; *V. lindheimeri* Rob. & Greenm., Blanco Co., Tex.; *V. microptera* DC., San Patricio Co., Tex.; *V. occidentalis* (L.) Walt., Clarke Co., Ga.; *V. rothrockii* Rob. & Greenm., Cochise Co., Ariz.; *V. virginica* L. (typical variety), Forest Co., Miss. and Poinsett Co., Ark.; *V. virginica* L. var. *laciniata* (Poir.) A. Gray, Taylor Co., Fla.; *V. walteri* Shinners, Allen Parish, La. All parental material showed very regular bivalent formation and pollen stainability, taken as a measure of male fertility, averaged above 85% in each case. Each species is diploid, $n = 17$, with the exception of *V. alternifolia*, which is tetraploid, $n = 34$.

Figure 1 presents a crossing diagram and summarizes those crosses which failed to result in F_1s; Figure 2 presents a crossing diagram summarizing those crosses which resulted in F_1s. Only species of the United States are included in the diagrams. Figures 3–12 present representative leaves of some of the species, and Figures 13–21 present representative leaves of some F_1s. Voucher material has been retained by the author.

[1]This study was supported by National Science Foundation Grants GB-13923 and GB-34129.

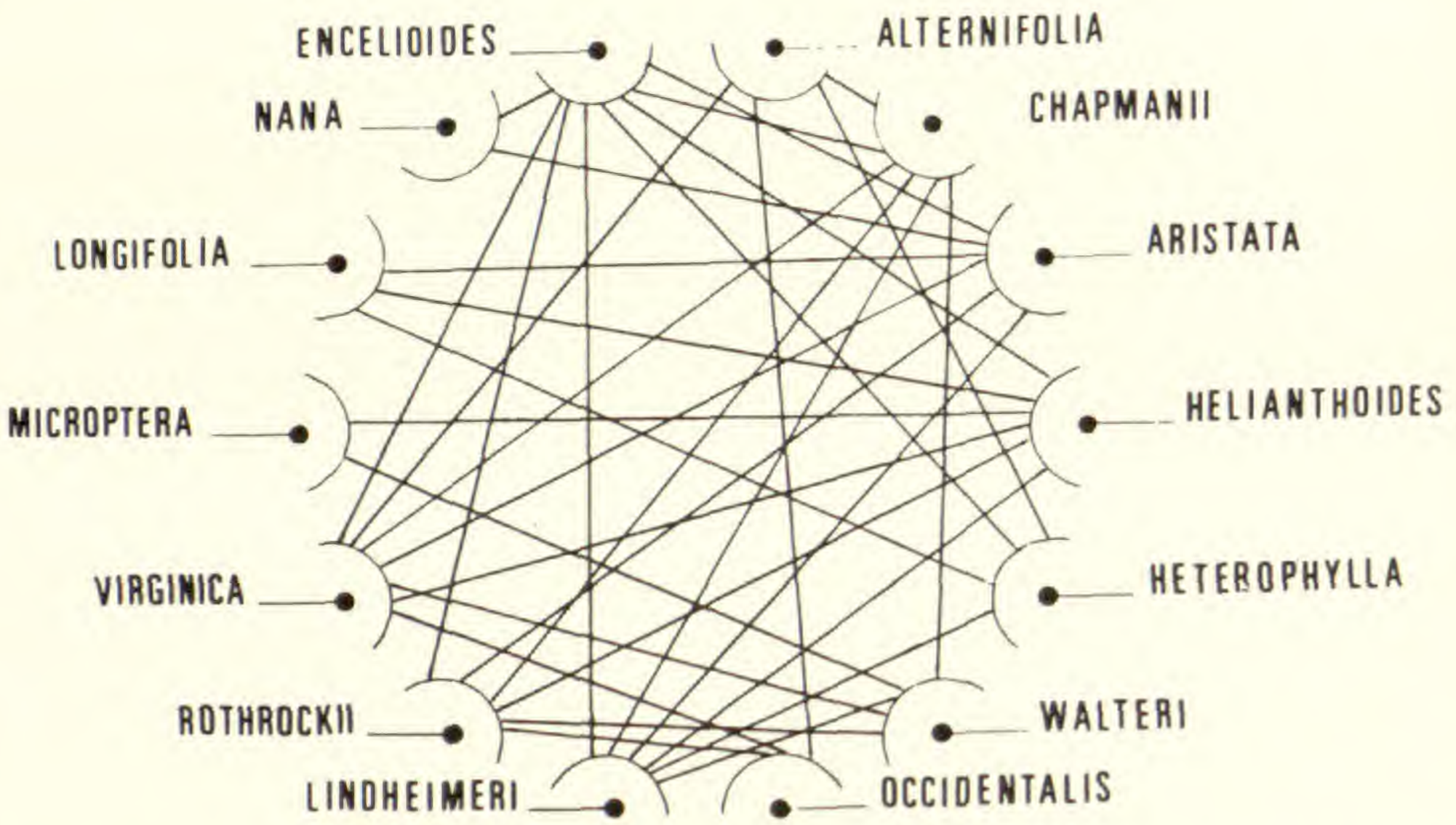


Figure 1. Diagram indicating crosses between United States species of *Verbesina* that failed to yield F_1 hybrids.

NEW HYBRIDS

Verbesina aristata × **V. glabrata.** Two plants were involved in this cross, and 3.5% of the 230 florets crossed formed full achenes. Two robust F_1s were obtained which had 1% and 7% pollen stainability. Chromosomes in the hybrids were sticky, and the five analyzable cells obtained showed 72% of the chromosomes associated in bivalents.

Verbesina glabrata reaches heights of 3–5 m and has oblanceolate leaves which frequently reach 20 cm in length and 5 cm in width. *Verbesina aristata* is generally less than 70 cm tall and has elliptic to elliptic-oblong leaves (Figure 3) mostly less than 8 cm long and 3 cm wide. The F_1s were nearly 1 m tall, with leaves tending toward those of *V. glabrata* in shape but toward those of *V. aristata* in size. Geographically, this is the widest cross achieved in *Verbesina*. *Verbesina glabrata* is a wide-ranging Brazilian species, whereas *V. aristata* is restricted to adjacent regions of Alabama, Georgia, and Florida.

Verbesina heterophylla × **V. occidentalis.** Two plants were involved in this cross, and 21% of the 205 florets crossed formed full achenes. The five F_1s were vigorous, but highly sterile with no plant having greater than 2% pollen stainability. One hundred and three cells of three F_1s were analyzed, and 28% of the chromosomes were associated in bivalents.

Verbesina heterophylla is mostly 50–70 cm tall, while *V. occidentalis* commonly exceeds 1.5 m. The F_1s were 80–95 cm tall. The leaves of *V. heterophylla* (Figure 4) are generally elliptic-oblong, 4–8 cm long, 2–3 cm wide, scabrous, and sessile. Those of *V. occidentalis* (Figure 5) are ovate, frequently exceed 20 cm in length and 8 cm in width, and are smooth and petiolate. Leaf shape of the F_1s (Figure 13) tended toward *V. occidentalis*, whereas leaf length was nearer to that of *V. heterophylla*. Roughness was intermediate, while the petiolate condition tended toward *V. occidentalis*. *Verbesina heterophylla* is restricted to the northeastern region of Florida, an area in which *V. occidentalis* is poorly represented, if it occurs at all.

Verbesina virginica × V. heterophylla. Six crossing combinations were made, and 1.4% of the 701 florets crossed formed full achenes. The single F_1 obtained was essentially fully sterile. Sixty-seven cells were analyzed, and 36% of the chromosomes were associated in bivalents.

Verbesina virginica frequently exceeds 1.5 m, whereas *V. heterophylla* is mostly less than 70 cm tall. The petiolate, ovate leaves of *V. virginica* (Figure 7) commonly attain 15 cm in length and 7 cm in width. The sessile, elliptic-oblong leaves of *V. heterophylla* (Figure 4) are mostly less than 8 cm long and 3 cm wide. The F_1 was intermediate in height with petiolate leaves which tended in shape toward those of *V. virginica* and approached those of that species in size (Figure 14). *Verbesina virginica* commonly has more than 100 heads per shoot, whereas those of *V. heterophylla* generally have many fewer than 20. Floret color is white in *V. virginica* and yellow in *V. heterophylla*. The F_1 had about 80 heads and white florets with some pinkish coloration. Both species occur in northeastern Florida and, although I have never seen a mixed population, it is possible that the species occur in sufficient proximity to permit intercrossing in nature.

Verbesina lindheimeri × V. rothrockii. Four crossing combinations were made, and 28% of the 496 florets crossed formed full achenes. Five vigorous F_1s were grown, and the single plant checked showed 77% pollen stainability. A study of 36 cells of three hybrids revealed 99% of the chromosomes associated in bivalents.

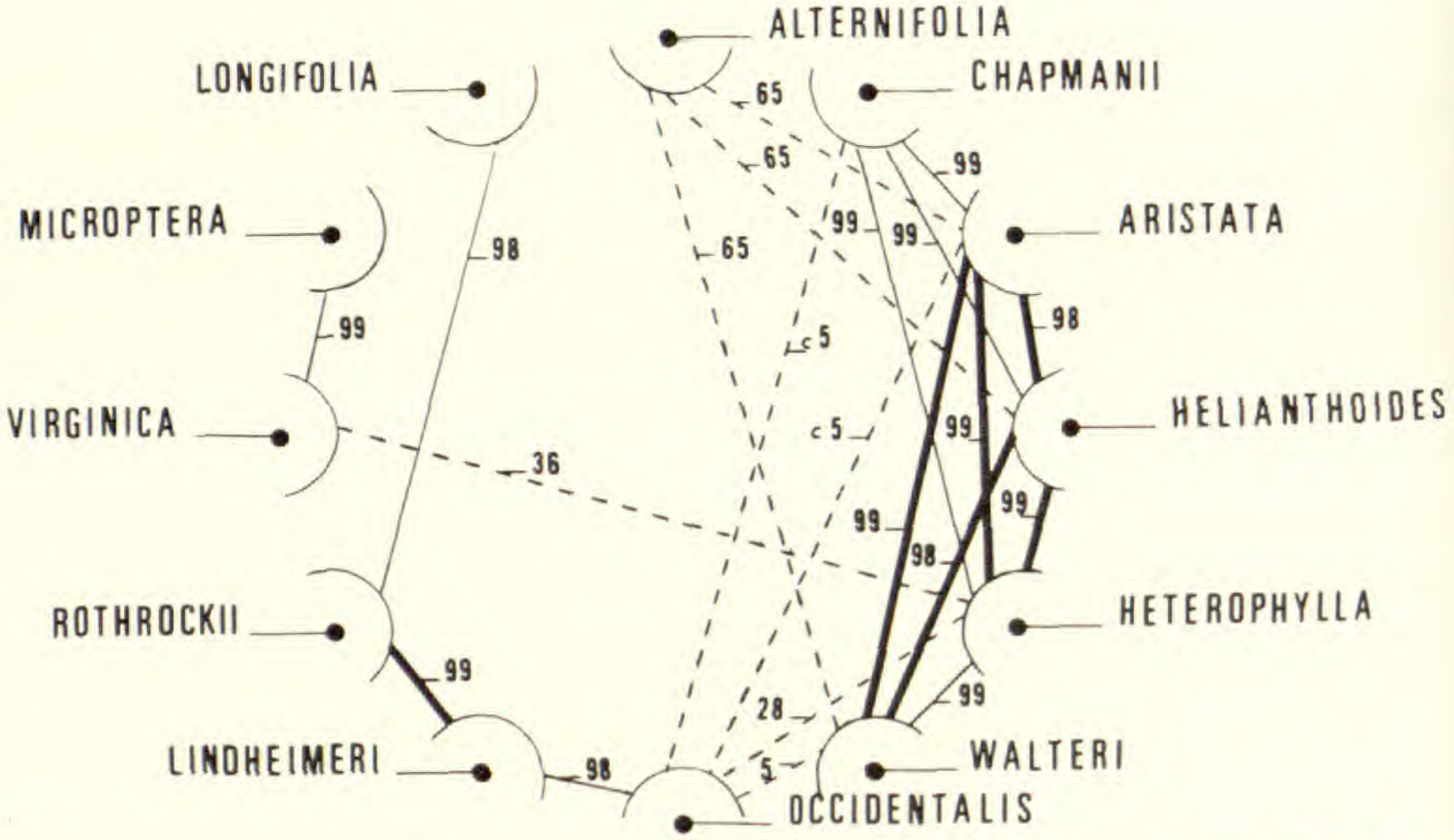


Figure 2. Diagram indicating crosses between United States species of *Verbesina* resulting in F_1 hybrids. Broken lines indicate F_1 hybrids with mean pollen stainability of 0%–20%, thin lines 45%–72%, and heavy lines 77%–99%. The number along the line is the percentage of F_1 chromosomes associated in bivalents, the remaining occurring as univalents.

Although readily separable, these species demonstrate a close morphological affinity. *Verbesina lindheimeri* has ovate, non-auriculate leaves (Figure 6) which frequently exceed 10 cm in length and 6 cm in width, whereas *V. rothrockii* has oblong or lance-oblong, mostly auriculate-based leaves, rarely to 9 cm in length and 4 cm in width. The F_1s were strongly intermediate. These species are allopatric. *Verbesina rothrockii* ranges from southern Arizona and southern New Mexico across northern Mexico, whereas *V. lindheimeri* is endemic to southcentral Texas.

Verbesina lindheimeri × **V. occidentalis.** Two plants were involved in the crossing, and 5.6% of the 244 florets crossed formed full achenes. The three vigorous F_1s had pollen stainability of 46%, 48%, and 62%, and the 83 cells studied revealed 98% of the chromosomes associated in bivalents.

Leaves of *Verbesina occidentalis* commonly exceed 20 cm in length, and are thin and smooth (Figure 5). *Verbesina lindheimeri* has leaves mostly less than 15 cm long which are thicker and strongly scabrous (Figure 6). Leaves of the F_1s (Figure 15) were intermediate in all respects. Flowering heads of *V. occidentalis* have mostly 2–4 rays and head diameter, less rays, is generally less than

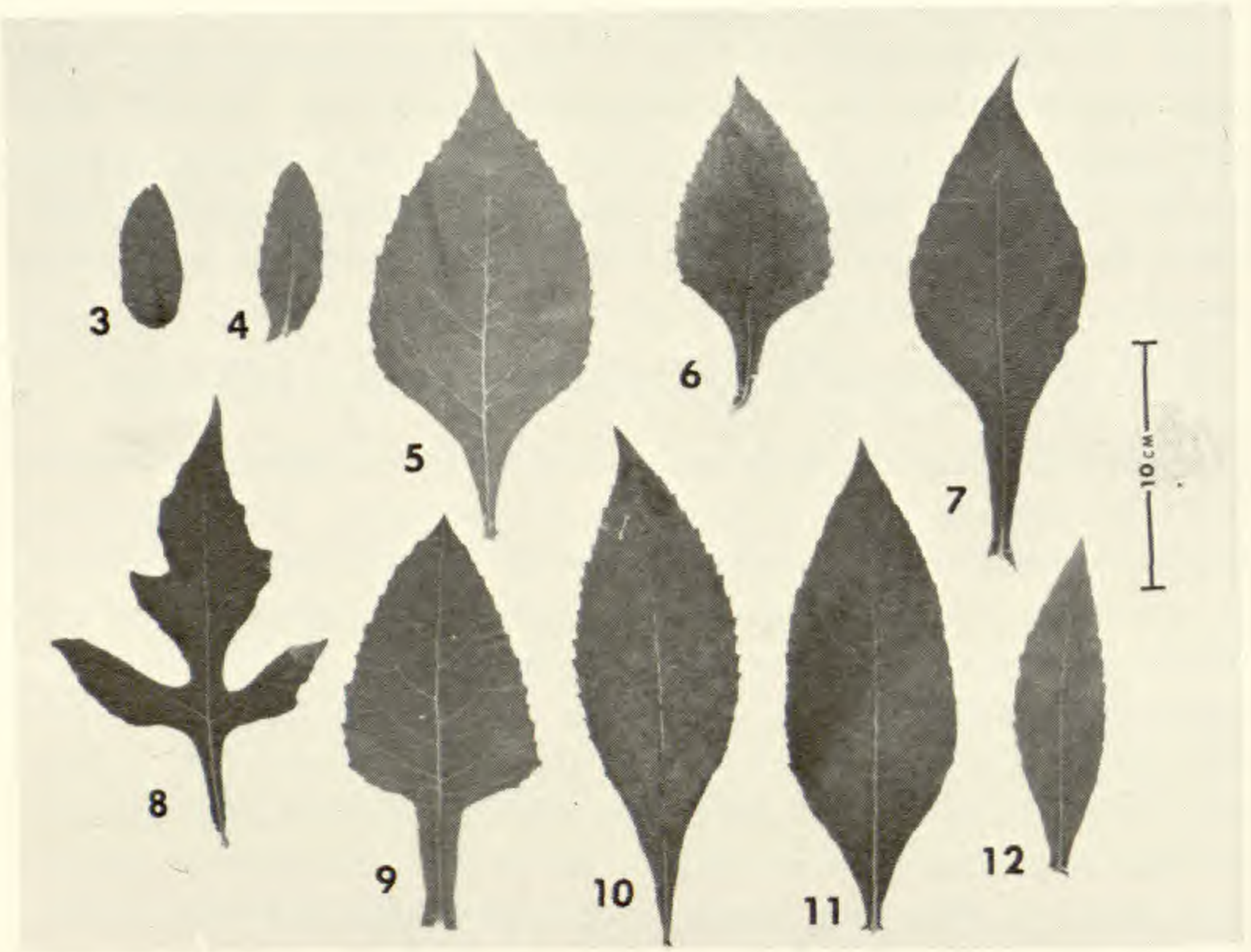
1 cm. *Verbesina lindheimeri* has mostly 10–12 rays per head, and head diameter, less rays, is mostly greater than 2 cm. The F_1s were intermediate for ray number and head size. These species are allopatric. *Verbesina lindheimeri* is endemic to southcentral Texas, whereas *V. occidentalis* is found throughout much of the eastern one-third of the country.

CROSSES WITHIN THE VERBESINA VIRGINICA COMPLEX

Verbesina virginica is a tall, white-flowered species common from Kansas to South Carolina and southward. The leaves are typically ovate with subentire to merely toothed margins (Figure 7). However, from coastal South Carolina into Florida they are frequently sinuately to deeply lobed (Figure 8) or, rarely, dissected. Since intergradation occurs between the various leaf forms, the lobe-leafed populations are usually treated as a variety, var. *laciniata* (Poir.) A. Gray, but have also been considered as a distinct species, *V. laciniata* (Poir.) Nutt. Two recent floras of the Southeast differ in their treatments. Radford, Ahles, and Bell (1964) treat the lobe-leafed form as a variety, while Long and Lakela (1971) treat it at the specific level.

Verbesina virginica typically has 1–5 rayed heads with distinct gaps occurring between the rays. However, populations clearly related to *V. virginica* occur in southern coastal Texas and adjacent Mexico and have mostly 10–12 rays per head, resulting in a more closed circle of rays. Some of these populations also have more deltoid leaves (Figure 9) and more numerously flowered heads than does typical *V. virginica*. These populations are generally accepted as a distinct species, *V. microptera* DC. However, Gray (1883) considered them conspecific with *V. virginica*, and Correll and Johnston (1970), while treating them as *V. microptera*, suggest their inclusion in *V. virginica*.

Crosses were made utilizing plants of two typical populations, one from Forest Co., Miss., and the other from Poinsett Co., Ark., a lobe-leafed population from Taylor Co., Fla., and a southern Texas population from San Patricio Co. A total of 23 plants was involved in the crossing. Mean achene set was fairly high for each cross, ranging from 30%–54%, and vigorous F_1s were obtained in each case. Mean F_1 pollen stainability was as follows: Miss. × Ark., 95% for five plants; Fla. × Miss., 93% for six plants; Tex. × Ark., 73% for seven plants; Tex. × Fla., 41% for twelve plants;



Figures 3–12. Representative leaves of some species of *Verbesina*. 3, *V. aristata*; 4, *V. heterophylla*; 5, *V. occidentalis*; 6, *V. lindheimeri*; 7, *V. virginica* (typical variety); 8, *V. virginica* var. *laciniata*; 9, *V. microptera*; 10, *V. walteri*; 11, *V. alternifolia*; 12, *V. helianthoides*.

Tex. × Miss., 73% for nine plants. About 30 cells were studied for each group of F_1s and, in each case, approximately 99% of the chromosomes were associated as bivalents. The hybrid nature of the F_1s was readily evident, except for those between the typical populations, which were very similar morphologically. F_1 leaf shapes were intermediate between those of the parental populations, and the F_1s formed with the Texas populations showed intermediacy in head size and ray number.

The close affinities suggested for these population systems on morphological grounds are substantiated by the close homology of their genomes and the generally high fertility of their F_1s. The lobe-leafed populations of the Southeast are probably more practically viewed as a variety of *Verbesina virginica*, whereas the southern Texas populations, although closely allied to *V. virginica*, are probably deserving of specific status.

Verbesina walteri × V. occidentalis. Six crossing combinations were made, and 13.7% of the 1042 florets crossed formed full achenes. The two F_1s grown were weak, chlorotic, and fully sterile. The 51 cells analyzed showed 5% of the chromosomes associated as bivalents.

Verbesina occidentalis has smooth, opposite, broadly ovate leaves which commonly exceed 8 cm in width and are three-nerved from the base of the blade (Figure 5). Those of *V. walteri* are subscabrous, alternate, narrowly elliptic, lanceolate, or oblanceolate, mostly less than 5 cm wide and pinnately nerved (Figure 10). The alternate, pinnately nerved leaves of the F_1s (Figure 16) were lance-elliptic to narrowly ovate, mostly less than 5 cm wide, and tended toward *V. occidentalis* in smoothness. The heads of *V. occidentalis* are elongate, rayed, and yellow-flowered, whereas those of *V. walteri* are globose, discoid, and white-flowered (Figure 22). Heads of the F_1s were intermediate in shape with rays which were essentially greatly elongated disc florets (Figure 23). F_1 floret color was initially yellow, but quickly faded to pale yellow, then white. The species are sympatric in South Carolina, but natural hybrids are unknown.

Verbesina alternifolia × V. helianthoides. Eleven crossing combinations were made, and 7.6% of the 2213 florets crossed developed full achenes. Successful crosses were obtained using *V. alternifolia* from Izard Co., Ark. Three robust, but fully sterile, triploids were grown. A study of 33 cells showed mostly 34 bodies per cell, indicating the presence of 17 bivalents and 17 univalents. However, occasional cells with 32 or 33 bodies suggest the possibility of occasional trivalents.

Verbesina alternifolia mostly exceeds 1.5 m in height, has leaves commonly exceeding 15 cm in length (Figure 11), and has globose heads (Figure 24) frequently exceeding 50 per shoot. *Verbesina helianthoides* is mostly less than 1 m tall, with leaves less than 15 cm long (Figure 12), and has campanulate heads (Figure 25), generally fewer than 10 per shoot. The F_1s were 70–80 cm tall, with the longest leaves to about 15 cm long (Figure 17), and had about 10 nearly globose heads per shoot. *Verbesina helianthoides* occurs from southwestern Ohio into northwestern Texas and is sympatric with *V. alternifolia* throughout most of its range. However, I know of no natural hybridization.

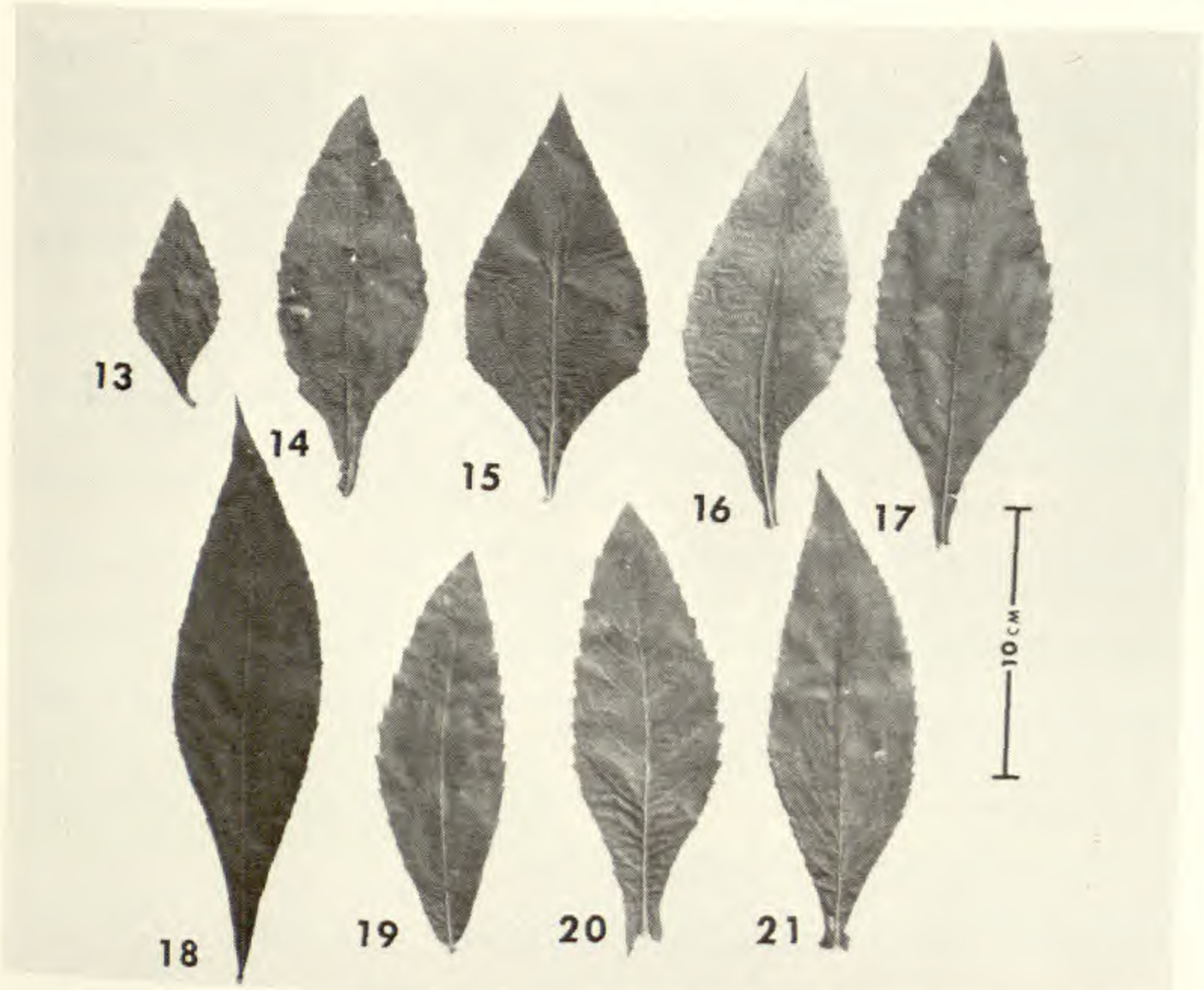
Verbesina walteri × **V. alternifolia.** Ten crossing combinations were made, and 7.6% of the 2044 florets crossed formed full achenes. The 13 triploid F_1s grown were vigorous but completely sterile. F_1s resulting from crosses using *V. alternifolia* from Montgomery Co., Md., showed a complete failure of the meiotic process, whereas those produced using *V. alternifolia* from Clarke Co., Ga., produced abnormal, mostly non-staining pollen. The 18 cells analyzed showed mostly 34 bodies, indicating a prevalent pairing configuration of 17 bivalents and 17 univalents. Although no definite trivalents were observed, occasional cells showing 32 or 33 bodies suggest their possible occasional occurrence.

The principal morphological differences between these species are that *Verbesina walteri* has glabrous stems and white-flowered, discoid heads (Figure 22), whereas *V. alternifolia* has hirsute stems and yellow-flowered, rayed heads (Figure 24). The F_1s were intermediate for stem pubescence and had rayed heads with the florets initially yellow, but fading to pale yellow, then white. Many rays had corolla tubes distinctly longer than pure *V. alternifolia*. F_1 leaf shape (Figure 18) tended toward *V. walteri*. These species occur sympatrically in Arkansas and possibly in Louisiana and the Carolinas, but natural hybrids are unknown.

THE HYBRID ORIGIN OF THE TETRAPLOID VERBESINA ALTERNIFOLIA

Verbesina alternifolia is one of the few tetraploid species reported for the genus. It and the closely related *V. walteri*, a diploid, have at times been separated to form the genus *Actinomeris* Nutt. These species share a combination of characters, globose heads and glaucous stems, not encountered elsewhere in the genus. Coleman (1971) demonstrated a close homology of the chromosomes of *V. walteri* and three unquestioned species of *Verbesina*, thereby supporting the inclusion of *V. walteri* and *V. alternifolia* in *Verbesina*.

In considering the parentage of *Verbesina alternifolia*, serious attention must be focused on *V. walteri* since this is the only extant species which could have contributed the combination of globose heads and glaucous stems. If *V. walteri*, which has white-flowered, discoid heads and glabrous stems, is in fact a genome donor to *V. alternifolia*, the second donor would be expected to have yellow-



Figures 13–21. Representative leaves of some interspecific F_1 *Verbesina* hybrids. 13, *V. heterophylla* × *V. occidentalis*; 14, *V. virginica* × *V. heterophylla*; 15, *V. lindheimeri* × *V. occidentalis*; 16, *V. walteri* × *V. occidentalis*; 17, *V. alternifolia* × *V. helianthoides*; 18, *V. walteri* × *V. alternifolia*; 19, *V. walteri* × *V. aristata*; 20, *V. walteri* × *V. heterophylla*; 21, *V. walteri* × *V. helianthoides*.

flowered, rayed heads and hirsute stems since these are the characters which best distinguish *V. alternifolia* from *V. walteri*. *Verbesina walteri* has been hybridized with three species having these characters: *V. aristata*, *V. heterophylla*, and *V. helianthoides* (Coleman, 1971). Leaves of the induced *V. walteri* × *V. aristata* F_1s (Figure 19) and the *V. walteri* × *V. heterophylla* F_1s (Figure 20) differ considerably from those of *V. alternifolia* (Figure 11). Furthermore, the stems of the *V. walteri* × *V. aristata* F_1s contrast with those of *V. alternifolia* by being wingless, and achene shape in the *V. walteri* × *V. heterophylla* F_1s differs strongly from that of *V. alternifolia*. However, the leaves of the induced *V. walteri* × *V. helianthoides* F_1s (Figure 21) compare favorably with those of *V. alternifolia* (Figure 11), as do head shape (Figures 24, 26), achene shape (Figure 27), stem pubescence, and most other charac-

teristics. *Verbesina helianthoides,* furthermore, is the only species of the three to occur sympatrically with *V. walteri*, and a natural *V. walteri* × *V. helianthoides* F_1 has been reported from Polk Co., Arkansas (Coleman, 1971). The principal morphological differences between *V. alternifolia* and the *V. walteri* × *V. helianthoides* F_1s are that F_1 floret color, although initially yellow, soon fades to pale yellow, then white, and the ray tubes are mostly longer than in *V. alternifolia*. Since the chromosomes of *V. walteri* and *V. helianthoides* are highly homologous, finely discriminatory preferential pairing would be essential for assuring fertility in doubled F_1s leading to the formation of *V. alternifolia*.

An additional diploid species, *Verbesina occidentalis*, has also been hybridized with *V. walteri*. *Verbesina occidentalis* satisfies the criteria of having rayed, yellow-flowered heads, but has glabrous or merely puberulent stems. The *V. walteri* × *V. occidentalis* F_1s compare well with *V. alternifolia* for leaf shape (Figures 11, 16), but differ in having much less pubescent stems, floret color fading to white, and by having mostly tubular rays which are essentially elongated disc florets (Figure 23). *Verbesina walteri* and *V. occidentalis* occur sympatrically in South Carolina, but I have never observed a natural F_1. Also, the induced F_1s were weak and chlorotic, and it is questionable whether natural F_1s could survive to maturity. The chromosomes of *V. walteri* × *V. occidentalis* are non-homologous, and preferential pairing of homologous genomes could be expected in doubled F_1s.

Both *Verbesina walteri* and *V. helianthoides* have been successfully crossed with *V. alternifolia*. In both cases the triploid F_1s exhibited mostly 17 bivalents and 17 univalents, suggesting that in each case the diploid genome was paired with one of the genomes of *V. alternifolia*. It cannot, however, be demonstrated whether the *V. helianthoides* and *V. walteri* genomes pair with the same or different genomes of *V. alternifolia*. It is also possible that the univalents in the triploids represent the diploid genomes, and that autosyndetic pairing occurs between the *V. alternifolia*

Figures 22–27. Flowering heads of some species and interspecific F_1 hybrids of *Verbesina*. 22, *V. walteri*; 23, *V. walteri* × *V. occidentalis*; 24, *V. alternifolia*; 25, *V. helianthoides*; 26, *V. walteri* × *V. helianthoides*; 27, achenes of *V. helianthoides* (A), *V. walteri* (B), *V. walteri* × *V. helianthoides* (C), and *V. alternifolia* (D).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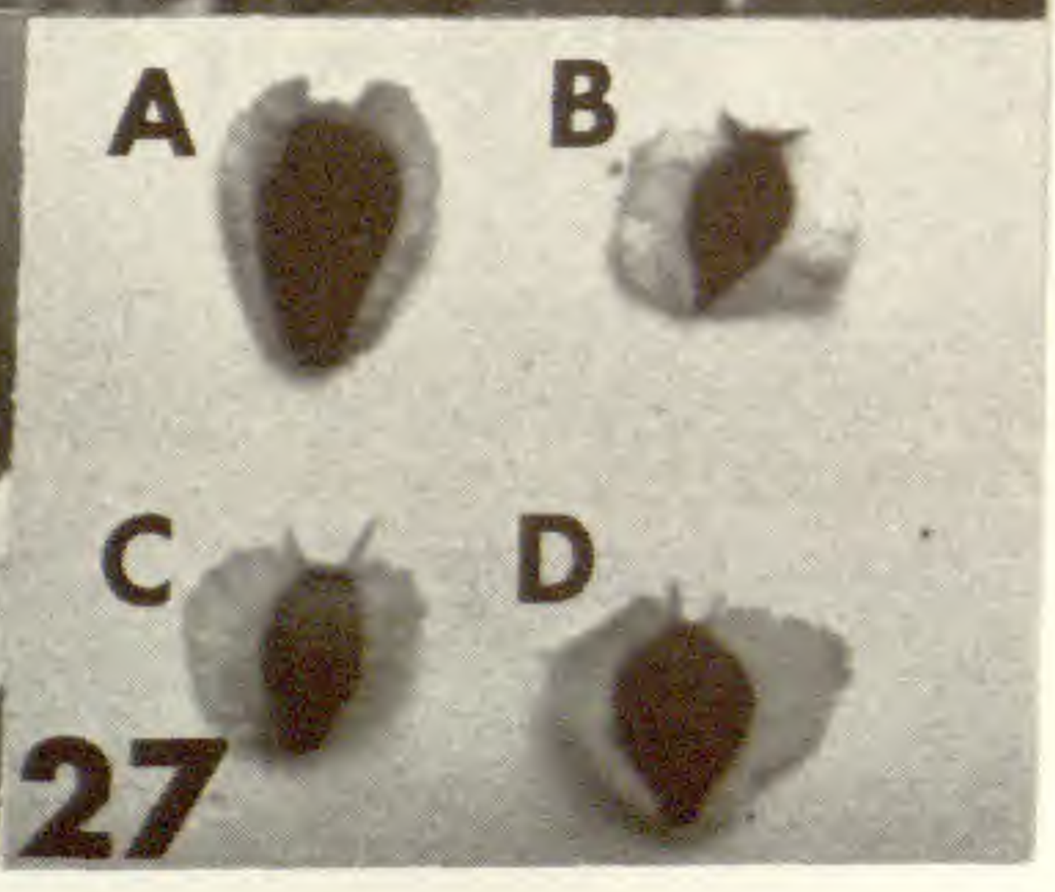

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genomes. However, the strong morphological evidence favoring the occurrence of the *V. walteri* genome in *V. alternifolia* tends to minimize this possibility.

The triploid hybrids provide genetic evidence that pale floret color in the *Verbesina walteri* × *V. helianthoides* F_1s is the result of dosage effect. Letting W represent the white allele of *V. walteri*, and w the yellow allele of *V. helianthoides*, and assuming an origin for *V. alternifolia* from the spontaneous doubling of the chromosome complement of *V. walteri* × *V. helianthoides* F_1s, the following plants would have the genotype given for the phenotype observed:

	Phenotype	Genotype
V. walteri	white	WW
V. helianthoides	yellow	ww
V. walteri × *V. helianthoides*	yellow, fading to white	Ww
V. alternifolia	yellow	WWww
V. walteri × *V. alternifolia*	yellow, fading to white	WWw
V. helianthoides × *V. alternifolia*	yellow	Www

Thus, the occurrence of a single w allele results in fading florets, whereas two w alleles gives persistently yellow florets. It is therefore reasonable to suggest that *Verbesina walteri* × *V. helianthoides* F_1s, following chromosome doubling, would have the genotype WWww, resulting in persistently yellow florets and plants very similar morphologically to *V. alternifolia*. Similarly, the fading florets of the *V. walteri* × *V. alternifolia* F_1 support the assumption that the white-flowered *V. walteri* is a parental species of *V. alternifolia*. Otherwise, *V. alternifolia* would be wwww, and the Www triploids might be expected to be persistently yellow-flowered.

The available evidence, although not conclusive, strongly suggests that *Verbesina alternifolia* evolved from hybridization between *V. walteri* and *V. helianthoides*, or similar extinct types, followed by spontaneous chromosome doubling in the F_1. Numerous attempts to achieve F_1 chromosome doubling with colchicine have been unsuccessful.

SECTIONAL LIMITS

In their revision of *Verbesina*, Robinson and Greenman (1899) expressed the opinion that many of their sections are artificial. Therefore, the results of the crossing program need to be considered in assessing sectional limits.

Robinson and Greenman treated *Verbesina chapmanii* Coleman (as *V. warei* A. Gray), *V. heterophylla*, and *V. aristata* in sect. *Pterophyton*, *V. helianthoides* in sect. *Verbesinaria*, and *V. walteri* in the genus *Actinomeris*. However, these species, each of which occurs in the eastern United States, can readily be hybridized to produce vigorous, fertile F_1 (Figure 2) and even F_2 and backcross hybrids (Coleman, 1971, 1974). Also, these species are strongly isolated from the remaining species in the program (Figure 1). A more natural treatment would consider these five species, along with *V. alternifolia*, as being consectional. Robinson and Greenman also included *V. rothrockii* and *V. lindheimeri*, both of the southwestern United States and Mexico, in sect. *Pterophyton*. Although these two species demonstrate a strong genetic interrelationship (Figure 2), they are strongly isolated genetically from the eastern species of sect. *Pterophyton* (Figure 1). It is therefore questionable whether they are naturally consectional with the eastern species.

Verbesina occidentalis was treated by Robinson and Greenman in the principally Mexican sect. *Verbesinaria*. Although this species can be successfully crossed with many of the eastern members of sect. *Pterophyton* (Figure 2), the hybrids demonstrate poor chromosome pairing and are highly sterile. However, *V. occidentalis* can readily be crossed with *V. lindheimeri* to form F_1s with excellent pairing and fair fertility. *Verbesina longifolia* A. Gray, another member of sect. *Verbesinaria*, hybridizes with *V. rothrockii*, again forming F_1s with excellent pairing and fair fertility (Figure 2). The homology of the chromosomes of *V. occidentalis* and *V. longifolia* with those of *V. lindheimeri* and *V. rothrockii* indicates closer affinities than have previously been suggested.

Verbesina virginica and *V. microptera*, both of sect. *Ochractinia*, demonstrate a close genetic interrelationship and are strongly isolated genetically from the remaining species (Figures 1, 2). *Verbesina encelioides* (Cav.) Benth. & Hook. f. and *V. nana* (Gray) Rob. & Greenm. compose sect. *Ximenesia*, and all attempts to hybridize them have failed (Figure 1).

CROSSING BARRIERS

The principal barrier to the formation of experimental hybrids was failure of interspecific achene formation. The successful germination of hybrid achenes was generally comparable to that of the parent species, and the F_1 generations, with a single exception, were vigorous, as were all F_2 and backcross hybrids grown.

Of the 14 crosses attempted between species which occur or probably occur sympatrically, five (36%) resulted in F_1s. Of these five F_1 populations, only one (20%) had mean pollen stainability exceeding 20% and 70% or more of the chromosomes associated in bivalents. Of the 41 crosses attempted between species which are probably or clearly allopatric, 16 (39%) yielded F_1s. Of these 16 F_1 populations 11 (69%) had mean pollen stainability exceeding 50%, and 12 (75%) had 95% or more of the chromosomes associated in bivalents. Thus, although experimental hybridization was equally successful between sympatric and allopatric species, F_1 fertility and chromosome homology were much greater for hybrids formed between allopatric species. Since those species capable of forming fertile F_1s, thereby permitting the possibility of later generation hybridization and interspecific gene exchange, rarely have contact, the primary reason for the minor role of natural hybridization in the United States species of *Verbesina* is evident.

Even among those species having the possibility of contact, mixed populations are unusual, explaining the rarity of even F_1s in nature. Spatially isolated species are generally thus maintained by numerous and complex ecological factors. The importance of edaphic factors in the spatial isolation of three northern Florida species has been demonstrated (Coleman, 1974).

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DEPARTAMENTO DE CIÊNCIAS BIÓLOGICAS
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE
SÃO JOSÉ DO RIO PRETO
ESTADO DE SÃO PAULO, BRASIL

A REVISION OF PECTIS SECTION PECTOTHRIX (COMPOSITAE: TAGETEAE)

DAVID J. KEIL

Pectis L. sect. *Pectothrix* A. Gray (Compositae: Tageteae) comprises a group of showy, yellow-headed species which occurs mainly in the arid and semi-arid portions of the southwestern United States and northern Mexico. Although several regional floras have included one or more of the species in this group, no workers since Fernald (1897) and Rydberg (1916) have attempted to treat this portion of the genus in its entirety. Since 1916, several workers have described new taxa (Cory, 1937; Johnston, 1940; Wiggins, 1951; Keil, 1974), and many new collections have been made. Recent studies (Keil, 1974) have suggested that the species relationships proposed by earlier workers (Fernald, 1897; Gray, 1884; Rydberg, 1916) should be re-examined.

TAXONOMIC HISTORY

The species included in the present report belong to a complex treated in the past as two subgenera, *Pectidopsis* and *Pectothrix* (Fernald, 1897). *Pectidopsis,* originally described as a monotypic genus (DeCandolle, 1836), was reduced in rank to a section of *Pectis* by Gray (1852), and was subsequently merged with sect. *Eupectis* by Gray (1884). Fernald (1897) resurrected *Pectidopsis* as a subgenus and included within it twelve species with the pappus coroniform and few-bristled or few-awned. *Pectothrix,* described by Gray (1849) as a subgenus of *Pectis,* was reduced to sectional rank three years later (Gray, 1852), but was returned to subgeneric level in Fernald's (1897) revision. Throughout its history, *Pectothrix* has been used for species with a multisetose pappus. Although Rydberg (1916), the last worker to revise this part of *Pectis,* did not accept any infrageneric categories, in most cases he retained the arrangement of species that Fernald had proposed.

RE-EVALUATION OF INFRAGENERIC BOUNDARIES

Previous investigators have emphasized in varying degrees the features of the pappus as characters for subdividing *Pectis,* first

into segregate genera (Lessing, 1830, 1831; DeCandolle, 1836), and later into sections or subgenera (Gray, 1849, 1852, 1884; Fernald, 1897). Although pappus characters can be used in some cases in conjunction with other features in delineating infrageneric categories in *Pectis* (e.g., sect. *Heteropectis* A. Gray), the use of these features alone, like any other one-character taxonomy, is subject to error. Fernald's *a priori* reliance upon pappus characters in his treatment of subgenera *Pectidopsis* and *Pectothrix* illustrates the problems of such an approach.

After field and herbarium studies of a number of the taxa included by Fernald in subg. *Pectidopsis* and subg. *Pectothrix*, I began to doubt the naturalness of these subgenera. Several lines of evidence led me to this viewpoint. First, the taxa included in subg. *Pectidopsis* sensu Fernald fall into two morphologically dissimilar groups which differ in several features (Table 1).

Table 1.

Morphological groups of Pectis subg. Pectidopsis sensu Fernald

CHARACTER	GROUP I	GROUP II
position of foliar oil glands	marginal	inframarginal or scattered
apex of immature capitula	rounded or truncate	narrowly conical, acute
number of ray florets	5 or 8	5
number of disc florets	10–40	5–10
pubescence of corollas	glandular-puberulent	glabrous

These two groups of taxa have different geographical and ecological ranges as well, with the taxa of Group I occurring in the arid and semi-arid areas of the southwestern United States and northern Mexico, and the species of Group II occupying a more southern distribution, extending well into the tropics of Mexico

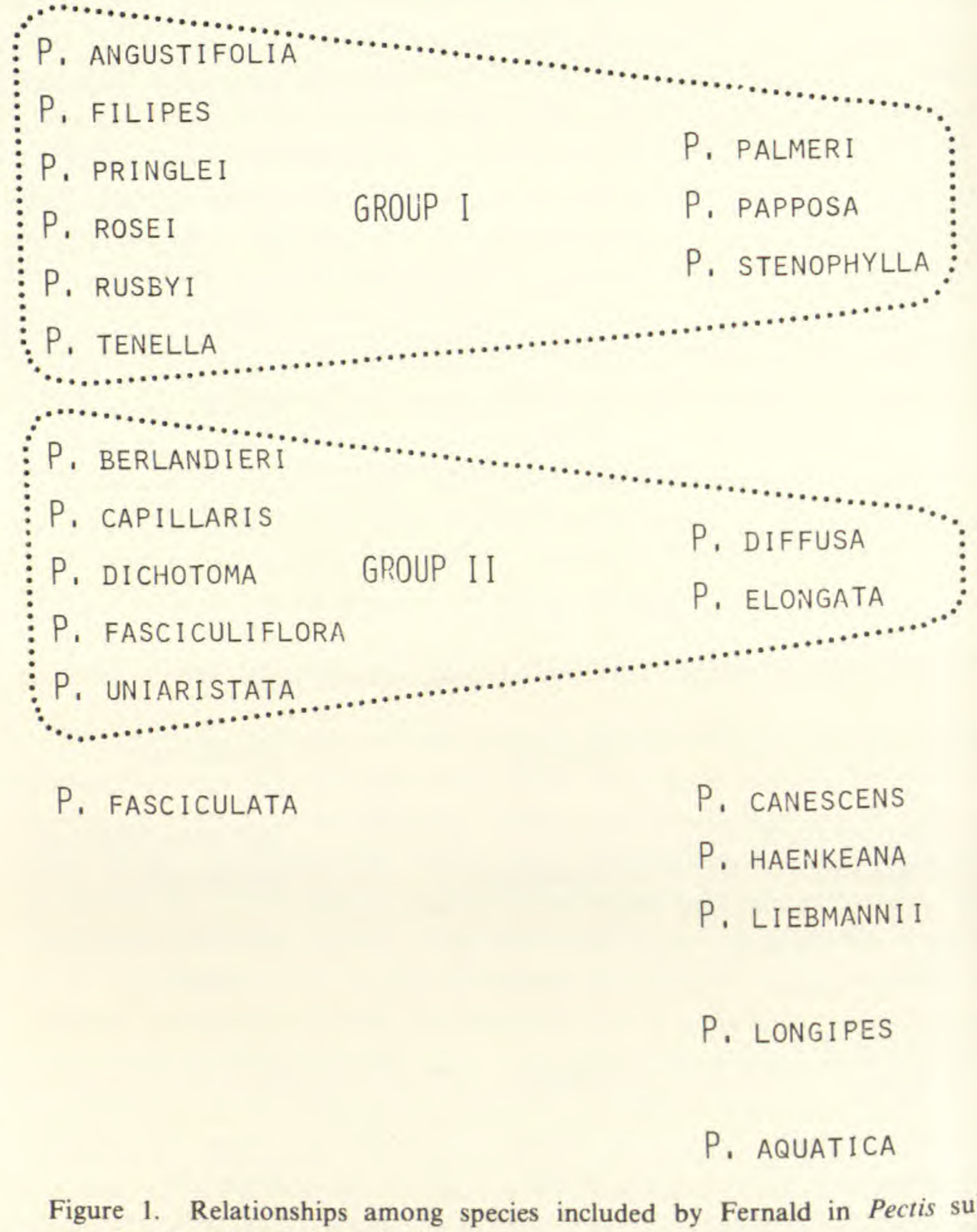

Figure 1. Relationships among species included by Fernald in *Pectis* subgenera *Pectidopsis* and *Pectothrix*.

and Central America. Second, if Fernald's taxonomy is followed, each of these groups of species has a counterpart in his subg. *Pectothrix*. Thus some species of subg. *Pectidopsis* appear to be more closely related to some species of subg. *Pectothrix* than they do to other species of their own subgenus (Figure 1).

The morphological similarity between taxa of different subgenera reflects the biological proximity of these species. Among the species of Group I (Figure 1), several cases of interspecific hybridization involving taxa from both subgenera have been observed (e.g., *Pectis papposa* × *P. angustifolia*, *P. papposa* × *P. filipes*). The hybrids are generally rather vigorous and fertile and evidence of backcrossing to the parent species has been found. This hybridization is an indication of the close relationship of the parent taxa. In one case, taxa of Fernald's different subgenera have even proved to be conspecific (*P. palmeri* of subg. *Pectothrix* is the same as *P. rusbyi* of subg. *Pectidopsis*).

A final line of evidence is the variability of the pappus itself. In some species (e.g., *Pectis angustifolia*, *P. papposa*, *P. rusbyi*), the pappus is sometimes so variable at the population level that the reliability of even infraspecific classifications, which rely on pappus structure, are doubtful.

Based upon this evidence, I have redrawn the infrageneric boundaries to reflect more accurately the species relationships. I have chosen to designate the newly defined infrageneric taxon for which the species of Group I (Figure 1) form a nucleus, as a section rather than as a subgenus. In rejecting the subgenus in favor of the section, I am following the lead of Gray (1884) who wrote concerning *Pectis:* "The genus is very natural; and, although two or three genera have been made from it, it seems incapable of division even into well-marked subgenera." In my opinion, the degree of differentiation among the species of *Pectis* is not sufficient to justify the recognition of subgenera.

The name, *Pectidopsis*, cannot be used for the newly defined section, because the provisions of Article 21 of the *International Code of Botanical Nomenclature* (Stafleu, 1972) prohibit its use at either the sectional or subgeneric level within *Pectis*. However, one of the two original species of sect. *Pectothrix* (for which no type species was ever designated), *P. papposa*, is now included in the section as I have defined it. I have designated *P. papposa* as the lectotype species of sect. *Pectothrix*, which is thus adopted as the name for the newly defined section. To the species of Group I (Figure 1), I have added several taxa described since Fernald (1897) published his revision. This group of taxa constitutes sect. *Pectothrix* as I am treating it.

The taxa which are included in Group II (Figure 1) constitute a distinct section not at all closely related to the species of the redefined sect. *Pectothrix*. This section, for which no name is known to be available, will be the subject of a future report. The remaining species which were included in subg. *Pectothrix* by Fernald are excluded from the present treatment. One of these, *Pectis aquatica*, is better treated as a member of a different genus, *Hydropectis*. The remaining species will be the subject of further investigations. *Pectis fasciculata*, the remaining species in subg. *Pectidopsis*, is a doubtful species of uncertain affinity for which I have been unable to locate a type. Unless or until a type is located for this species, I will exclude it from further consideration.

TAXONOMIC TREATMENT

Pectis L. sect. **Pectothrix** (A. Gray) A. Gray, Smithsonian Contr. Know. **3:** 83. 1852. LECTOTYPE SPECIES (here designated): *Pectis papposa* Harv. & Gray in A. Gray.

Pectis subg. *Pectothrix* A. Gray, Mem. Am. Acad. **4:** 62. 1849.
Helioreos Raf., Atlantic Jour. **1:** 145. 1832. TYPE SPECIES: *Pectis angustifolia* Torrey.
Pectidopsis DC., Prodr. **5:** 98. 1836, nom. illeg. (superfluous when published).
Pectis sect. *Pectidopsis* (DC.) A. Gray, Smithsonian Contr. Knowl. **3:** 83. 1852, nom. illeg.
Pectis subg. *Pectidopsis* (DC.) Fern., Proc. Am. Acad. **33:** 72. 1897, nom. illeg.

Glabrous or pubescent annual or perennial usually strong-scented herbs. Stems erect to prostrate, one to many from the base, much-branched above. Leaves linear to elliptic or oblanceolate (pinnatifid in one species), ciliate toward the base with one–several pairs of bristles, punctate with conspicuous marginal oil glands or, in some 8-rayed species, with inframarginal glands on the undersurface. Heads in open to condensed cymose clusters, subsessile or on peduncles up to 13 cm long. Immature heads mostly truncate or broadly rounded. Phyllaries usually either 5 or 8, linear to narrowly obovate, obtuse to acutish, strongly carinate, narrowly to broadly hyaline-margined, variously punctate, not or scarcely imbricate, falling individually at maturity. Ray florets 5 or 8; corollas spreading, showy, bright yellow, usually glandular-puberulent below. Disc florets (5–) 10–60; corollas bright yellow, 5-toothed, regular or somewhat bilabiate, usually glandular-puberulent below. Achenes cylindrical, many-ribbed, variously

pubescent, black. Pappus coroniform and/or setose or aristate, the ray pappus often differing from the disc pappus. Chromosome base number: $x = 12$.

DISTRIBUTION: California and Nebraska south to the Mexican states of Sinaloa, Aguascalientes, and San Luis Potosí; one species disjunct in Peru. Locally abundant throughout much of the arid and semi-arid portion of North America from sea level to 2000 m.

KEY TO THE TAXA OF PECTIS SECTION PECTOTHRIX

1. Phyllaries and rays 8 (rarely 7, 9 or 10). ..... 2.
   2. Leaves pinnatifid. ..... 7. *P. incisifolia.*
   2. Leaves entire or nearly so. ..... 3.
      3. Inflorescence rather congested; peduncles mostly less than 15 mm long. ..... 4.
         4. Pappus bristles (if present) sub-plumose; trichomes on achenes with curled bulbous tips; leaf bases not flared. ..... 5.
            5. Phyllaries 3–5 mm long; disc florets 6–14; disc pappus 1.5–2.5 mm long. ..... 4a. *P. papposa* var. *papposa.*
            5. Phyllaries 5–8 mm long; disc florets 12–24 (–34); disc pappus 2.5–4 mm long. ..... 4b. *P. papposa* var. *grandis.*
         4. Pappus bristles (if present) short scabrid; trichomes on achenes with straight, bifurcate tips. ..... 6.
            6. Bases of upper leaves conspicuously flared, often partially concealing the peduncles; pappus usually only coroniform (weakly aristate or few-setose in some Texan or Chihuahuan populations); plants usually lemon-scented when fresh. ..... 5a. *P. angustifolia* var. *angustifolia.*
            6. Bases of upper leaves seldom flared; pappus mostly 1–7 aristate or setose (though sometimes reduced to a low crown); plants usually spicy-scented. ..... 7.
               7. Phyllaries broadest near the middle, with a subterminal oil gland less than 0.5 mm long; pappus bristles often exceeding 1 mm; plants always annual; widespread in south Texas and Mexico. ..... 5b. *P. angustifolia* var. *tenella.*
               7. Phyllaries broadest near the apex, with a subterminal oil gland 0.5–1 mm long; pappus usually less than 1 mm long; plants annual or perennial; endemic to the Edwards Plateau area of central Texas. ..... 5c. *P. angustifolia* var. *fastigiata.*
   3. Inflorescence open; peduncles more than 15 mm long. ..... 8.
      8. Phyllaries broadly obtuse, usually conspicuously longitudinally striate; disc pappus of about 20 bristles or rarely reduced to a crown of short scales; ray pappus biaristate. ..... 2. *P. rusbyi.*

8. Phyllaries either not broadly obtuse or not longitudinally striate. .... 9.
9. Pappus of disc achenes 1–4 aristate, the awns slender, 2–4 mm long; achenes 3–4.5 mm long. ..... 6. *P. pringlei.*
9. Pappus either not aristate or achenes shorter. ..... 10.
10. Ray pappus coroniform or multisetose. ..... 11.
11. Ray pappus coroniform. ..... 12.
12. Disc pappus usually setose; foliar oil glands marginal. ..... 4b. *P. papposa* var. *grandis.*
12. Disc pappus coroniform; foliar oil glands inframarginal on the undersurface. ..... 8a. *P. purpurea* var. *purpurea.*
11. Ray pappus multisetose; plants of Peru. ..... 3. *P. peruviana.*
10. Ray pappus biaristate (sometimes with one or more short scales between the awns). ..... 13.
13. Leaves broadly elliptic or oblanceolate, obtuse, mostly 6–12 mm broad; endemic to coastal areas of southern Sinaloa. ..... 9. *P. sinaloensis.*
13. Leaves linear to narrowly elliptic or oblanceolate, mostly acute to acutish, usually less than 6 mm wide. ..... 14.
14. Ray corollas 7–12 mm long; pappus biseriate. .... 15.
15. Outer pappus of disc achenes of slender bristles; leaves with 1–3 pairs of marginal cilia; foliar oil glands in submarginal rows. ..... 8b. *P. purpurea* var. *sonorae.*
15. Outer pappus of flattened, fimbriate pales; leaves usually with 4–6 pairs of marginal cilia; foliar oil glands submarginal and scattered on the undersurface. ..... 8c. *P. purpurea* var. *lancifolia.*
14. Ray corollas 2–6 mm long. ..... 16.
16. Plants perennial with a stiff woody caudex. ... 17.
17. Herbage glabrous or nearly so. ..... 1a. *P. stenophylla* var. *stenophylla.*
17. Herbage densely hirtellous. ..... 1b. *P. stenophylla* var. *gentryi.*
16. Plants annual without a woody caudex. ..... 18.
18. Heads mostly broadly campanulate, 17–26 flowered. ..... 1e. *P. stenophylla* var. *biaristata.*
18. Heads narrowly campanulate to cylindrical, 8–17 flowered. ..... 19.
19. Herbage glabrous; leaves very narrow, mostly less than 1 mm wide. ..... 1c. *P. stenophylla* var. *rosei.*
19. Herbage densely hirtellous; leaves often more than 2 mm wide. ..... 1d. *P. stenophylla* var. *puberula.*

1. Ray florets 5 (rarely 4 or 6). ..... 20.
   20. Phyllaries 3.5–6 mm long; disc corollas 2.5–4 mm long; pappus 0–3 aristate. ..... 21.
      21. Fascicles of small leaves usually present in the upper leaf axils; peduncles mostly 10–25 mm long; disc florets 2–8; plants of central and southern Sonora. ..... 10a. *P. filipes* var. *filipes*.
      21. Fascicles of leaves usually absent; peduncles mostly 20–50 mm long; disc florets 7–22; plants with more northern or eastern distribution. ..... 10b. *P. filipes* var. *subnuda*.
   20. Phyllaries 6–8 mm long; disc corollas 4–5 mm long; pappus 2–6 aristate; plants of Baja California. ..... 11. *P. vollmeri*.

1. **Pectis stenophylla** A. Gray, Proc. Am. Acad. **21:** 393. 1886. TYPE: **Mexico.** CHIHUAHUA: near Batopilas, *Palmer 81* (Holotype, GH!; isotypes, K!, PH!). Figure 2.

Annual or perennial herbs from a slender taproot or woody caudex. Stems 10–30 cm long, one to many from the base, erect or decumbent, glabrous to densely hirtellous, ciliate with 1–3 pairs of basal bristles 1–3 mm long, punctate marginally with golden-brown oil glands or, in some forms, punctate submarginally on the undersurface with tiny black glands 0.1–0.2 mm diameter. Peduncles filiform, 2.5–7 cm long, glabrous or hirtellous; bracteoles 3–8, linear to lanceolate, glabrous or hirtellous, sometimes punctate. Heads terminal or axillary; involucres campanulate. Phyllaries linear to oblong, 3.5–5.5 mm long, 0.5–2 mm broad, obtuse to acutish, basally rounded and gibbous, slender-keeled nearly to the apex, glabrous to hirtellous, punctate with 1 or 2 subterminal and 2–3 pairs of slender submarginal glands, these either brown and swollen or tiny and black. Ray florets 8; corollas 2–6 mm long, yellow or becoming tinged reddish, with ligules glabrous and tubes glandular-puberulent. Disc florets 8–26, bilabiate, 1.7–3 mm long, glandular-puberulent. Achenes 1–2.5 mm long, strigillose. Pappus of the ray achenes biaristate, 1–2 mm long; pappus of the disc achenes variable, setose, aristate, and/or coroniform, 1–2 mm long. Chromosome number (from var. *biaristata* only): $n = 12$.

DISTRIBUTION: Eastern Sonora and southwestern Chihuahua to central Sinaloa and western Durango, from 300 to 1500 meters elevation. Very local in thorn forest and oak forest zones (Figure 3).

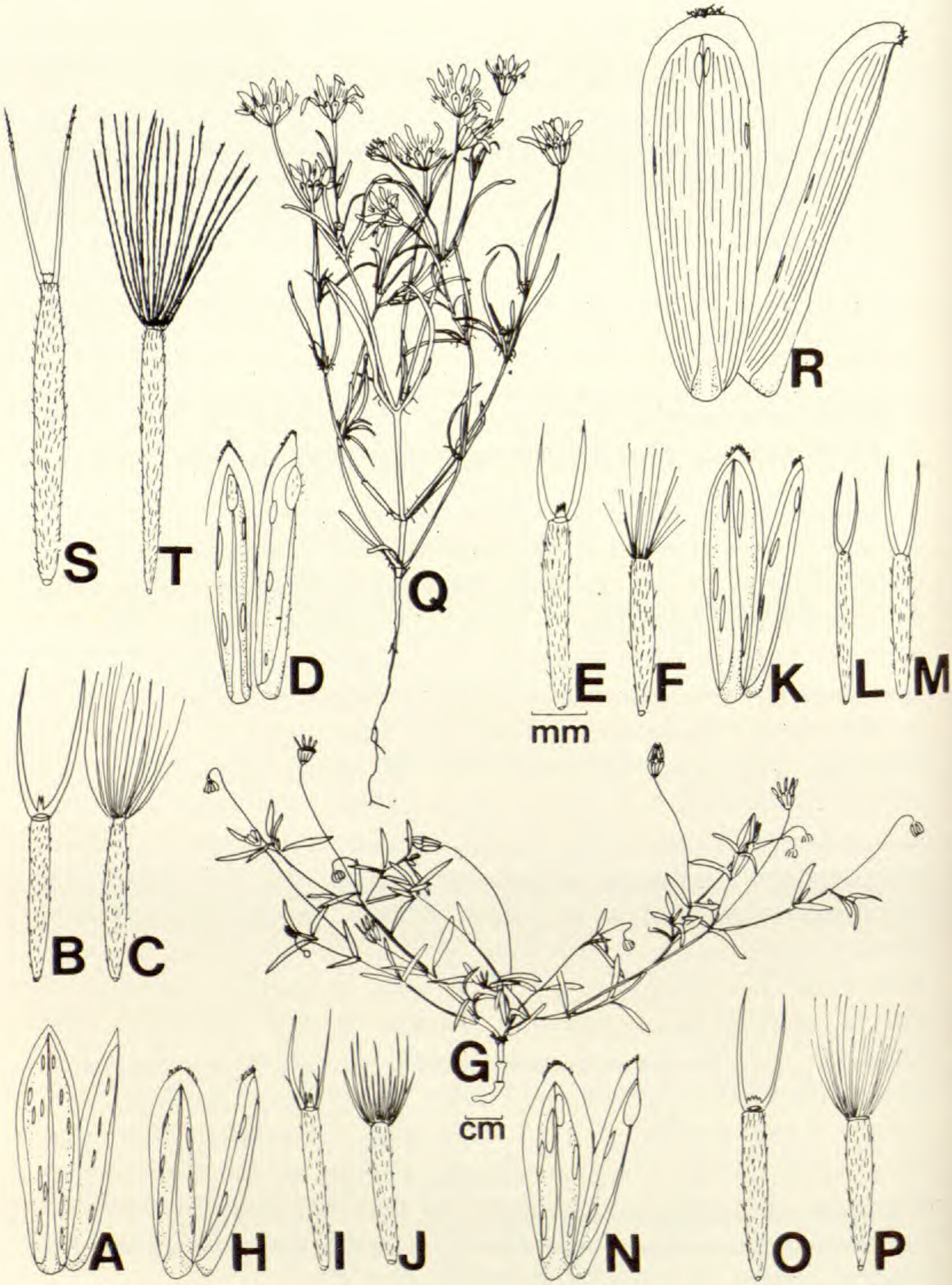

Figure 2. A-P, *Pectis stenophylla;* A-C, var. *biaristata* (*Keil & Canne 8752,* OS); D-F, var. *gentryi (Gentry 7323,* MICH); G-J, var. *puberula* (*Gentry 5495,* NY); K-M, var. *rosei* (*Palmer 730,* GH); N-P, var. *stenophylla* (*Kimnach & Brandt 950*); Q-T, *Pectis rusbyi.* A, D, H, K, N, R, phyllaries; B, E, I, L, O, S, ray achenes; C, F, J, M, P, T, disc achenes; G, Q, habit.

Pectis stenophylla is an unusually variable species. Local races, isolated from other populations, often by considerable distances, have undergone marked divergence. In 1916 Rydberg recognized a total of five species from this complex, a logical treatment based upon the limited samples then available. Each taxon, however, was known from only one or two collections.

In the intervening period since Rydberg's treatment, a number of collections from additional populations have been made. Members of several of these populations have character combinations intermediate to those of species accepted by Rydberg. Because of this observed intermediacy, I have chosen to regard all members of this complex as one polymorphic species and to recognize the variant forms at the varietal level. The species thus defined is comparable to other variable species within sect. *Pectothrix*.

Some objection might be raised to the inclusion of the perennial *Pectis stenophylla,* sensu stricto, in the same species with several annual forms. There is, however, precedent and ample justification for such a treatment. Both perennial and annual forms exist in another species of the section, *P. angustifolia,* and a tendency toward the perennial habit is found in some annual species of other sections (e.g. some populations of *P. prostrata* of sect. *Pectis*). In one population of *P. stenophylla* var. *puberula* (*Gentry 5282*), annuals and apparently perennial forms occurred together, thus indicating the plasticity of the habit in these plants.

One feature of particular interest in *Pectis stenophylla* is the vestigial nature of the oil glands in some local races. Collectors' notes on herbarium labels indicate that the oils of plants with swollen brown glands are quite aromatic. In some populations, however, the glands are small, dark brown or black, and shrunken, and apparently lack any detectable odor (personal observation). The odorless glands are apparently displaced from the leaf margin during ontogeny. This relationship is quite apparent from an examination of the type collection of *P. scabra,* in which plants with either one or the other type of oil glands coexisted in the same population. Those foliar oil glands that are tiny and black are inframarginal on the undersurface of the leaves. Because this variation can occur within a population, I consider the taxonomic significance of this character to be of minor importance in *P. stenophylla*.

1a. **Pectis stenophylla** A. Gray, Proc. Am. Acad. **21:** 393. 1886. var. **stenophylla.** Figure 2.

Plants perennial. Stems 15–25 cm long, woody and rigid at the base, glabrous or nearly so. Leaves linear, 1–3 cm long, 1–2 mm wide, glabrous, marginally punctate with golden-brown oil glands. Peduncles 2.5–5 cm long, glabrous. Phyllaries 4–4.5 mm long, 1 mm wide, punctate with a conspicuously enlarged subterminal oil gland and smaller submarginal glands. Ray corollas 4–6 mm long. Pappus of the rays 1.5–2 mm long; pappus of the disc 10–20 setose, 1–2 mm long. Chromosome number unknown. Flowering August to April.

DISTRIBUTION: Eastern Sonora and southwestern Chihuahua at 600 to 1500 meters elevation (Figure 3).

In some areas the local residents boil the herbage of *Pectis stenophylla* and use the decoction as a medicine (Gentry, 1942). Since the plants of var. *stenophylla* are not very common (as evidenced by the paucity of collections), such usage, if very common, must put a considerable strain on the populations of this taxon. In species with large population systems, local harvesting is probably of little overall significance. For a taxon as uncommon as var. *stenophylla,* however, man's influence may have profound effects.

REPRESENTATIVE SPECIMENS[2]: **México.** CHIHUAHUA: Río Batopilas, *Kimnach & Brandt 950* (US); Guagueybo, *Pennington 42* (TEX). SONORA: San Bernardo, *Gentry 1025* (F, GH, MO); San Bernardo, *Gentry 1358* (MICH); Arroyo Hondo, *Hartman 216 p. p.* (GH); Bacadehuachi, *Lloyd 402* (GH).

1b. **Pectis stenophylla** A. Gray var. **gentryi** Keil, var. nov. Figure 2.

TYPE: **Mexico.** SINALOA: Varomena and vicinity, *Gentry 7325* (Holotype, GH!; isotypes, F!, MICH!, NY!).

Plantae perennes. Caules 15–30 cm longi, basi lignosi rigidesque, dense hirtelli. Folia linearia vel anguste elliptica, 1–2 cm

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[2]Unless a taxon is known from very few collections, only widely distributed or otherwise important specimens are cited. The following abbreviations are used for the collectors of specimens prepared during the present study: *K = Keil, K & M = Keil & McGill,* and *K & C = Keil & Canne.* Because duplicates of some of the collections made during the preparation of this study are still being distributed, only the herbarium of the Ohio State University (OS) is listed for those collections.

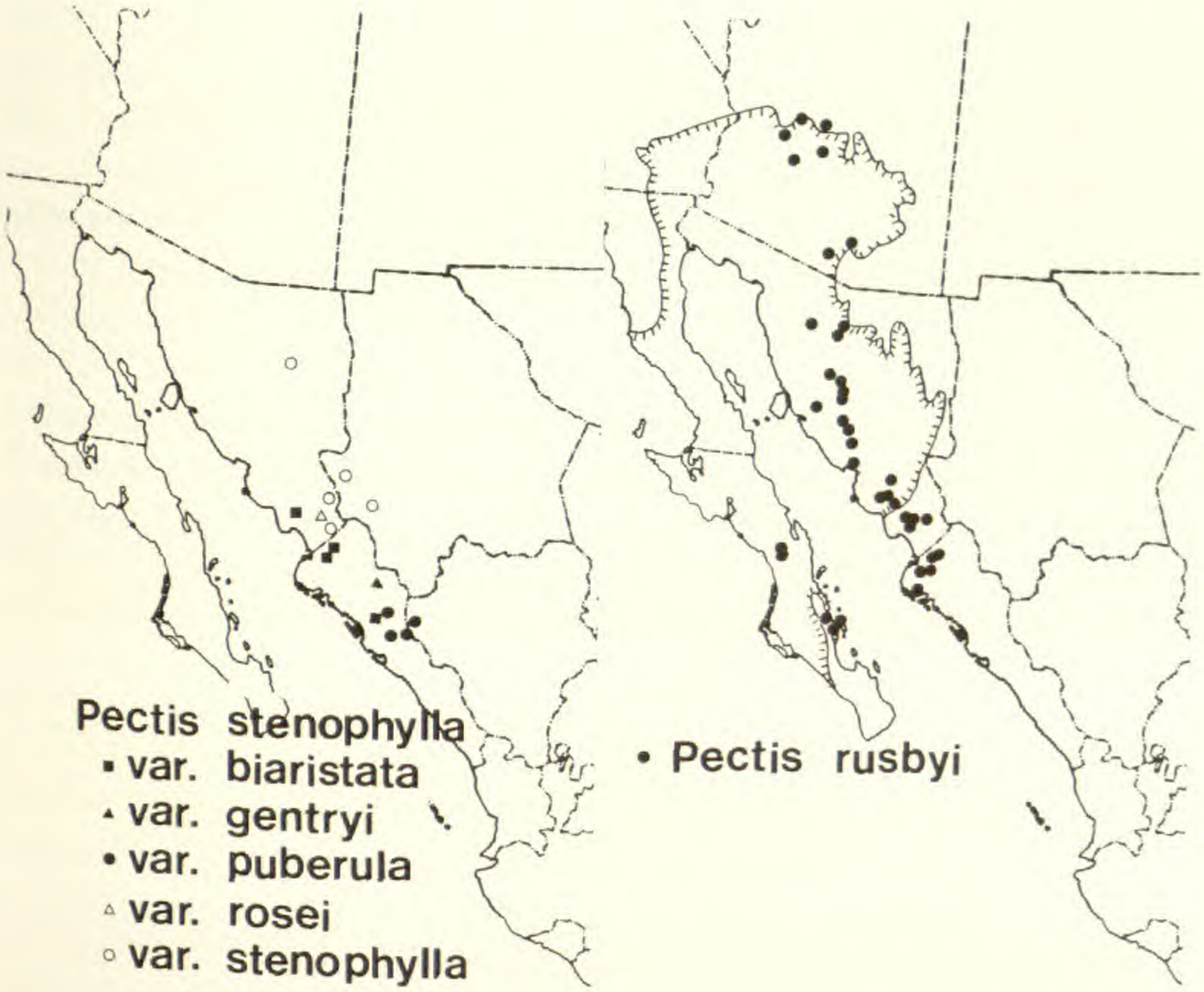


Figure 3. Geographical distribution of *Pectis stenophylla* and *P. rusbyi.* Half-barred line indicates Sonoran Desert boundary (redrawn from Shreve, 1942).

longa, 1–3 mm lata, dense hirtella, margine punctata. Pedunculi 3–5 cm longi, hirtelli vel glabrescentes, 3–5 bracteolati. Phyllaria 4–4.5 mm longa, dense hirtella. Corollae flosculorum radiorum 4 mm longae. Flosculi disci 8–10, corollis 2.5–2.7 mm longis. Achenia 2.5 mm longa. Pappus radiorum biaristatus, 1.5 mm longus; pappus discorum circa 20–setosus, 1–2 mm longus. Chromosomatum numerus ignotus.

DISTRIBUTION: Known only from the type locality in northern Sinaloa at 300 meters elevation (Figure 3).

Gentry's collection is from the Sierra Surotato, a mountain mass isolated from the main cordillera of the Sierra Madre Occidental by a distance of about 40 miles (Gentry, 1946). This plant differs from the more northern var. *stenophylla* in being densely scaberulous rather than almost completely glabrous. In addition, the leaves appear to be mostly shorter and thicker in var. *gentryi* than in var. *stenophylla.*

1c. **Pectis stenophylla** A. Gray var. **rosei** (Fern.) Keil, comb. nov. BASIONYM: *Pectis rosei* Fern., Proc. Am. Acad. **33:** 77. 1897. TYPE: **Mexico.** SONORA: Alamos, *Palmer 730* (Holotype, GH!; isotype, US!; photo of US isotype, NY!). Figure 2

Plants annual. Stems 20–30 cm long, glabrous. Leaves linear, 2–3 cm long, 1 mm wide, strongly revolute, glabrous, punctate on the undersurface with tiny black glands. Peduncles 3–5 cm long, glabrous. Heads cylindric. Phyllaries very narrowly linear, 3.5–4 mm long, ca 0.5 mm broad, punctate with linear red-black glands. Ray corollas 3 mm long. Disc florets 11–12; corollas 2 mm long. Achenes 2 mm long. Pappus of the rays 1–1.5 mm long; pappus of the disc 2–3 aristate, ca 1.5 mm long. Chromosome number unknown.

DISTRIBUTION: Known only from the type locality in southern Sonora at ca. 1500 meters elevation (Figure 3).

Pectis stenophylla var. *rosei* is perhaps most closely related to var. *stenophylla,* which it resembles in being glabrous and in having very narrow leaves. The two differ in habit, foliar oil glands, and pappus structure. Since var. *rosei* is still known only from its type collection, the full range of variation remains unknown.

1d. **Pectis stenophylla** A. Gray var. **puberula** (Greenm.) Keil, comb. nov. BASIONYM: *Pectis puberula* Greenm., Proc. Am. Acad. **40:** 49. 1904. TYPE: **Mexico.** SINALOA? Lodiego, *Palmer 1605* (Syntypes, GH!, US!; isosyntypes, F!, GH!, NY!; lectotype (here chosen), syntype at GH). Figure 2.

Pectis scabra Brandeg., Zoe **5:** 226. 1906. TYPE: **Mexico.** SINALOA: Cofradia, *Brandegee s.n.* (Holotype, UC!; isotypes, GH!, POM!, US!).

Plants annual, or sometimes persisting more than one growing season. Stems 10–30 cm long, sparsely to densely hirtellous. Leaves linear to narrowly elliptic, 1–4 cm long, 1–5 mm wide, densely hirtellous, punctate either marginally with golden-brown glands or on the abaxial surface with tiny black glands. Peduncles 3–6 cm long, glabrous to puberulent, 3–6 bracteolate. Heads cylindric to narrowly campanulate. Phyllaries 3–4.5 mm long, glabrous to densely hirtellous, punctate with either brown or black

glands. Ray corollas narrow, 2–3.7 mm long. Disc florets 8–17; corollas 1.7–3 mm long. Achenes 1–2.5 mm long. Pappus of the rays 1–1.5 mm long; pappus of the disc coroniform, 2–4 aristate or 10–20 setose, highly variable, 1–2 mm long. Chromosome number unknown. Flowering October to March.

DISTRIBUTION: Central Sinaloa and western Durango at 200 to 900 meters elevation (Figure 3).

The pappus of var. *puberula* is highly variable. Within populations from both the type locality of *Pectis puberula* (*Palmer 1605*) and from the type locality of *P. scabra (Gentry 5495*), a full range from coroniform to short aristate to setose pappus forms occurs. *Pectis scabra* and *P. puberula* were described from different pappus forms. Although the exact locality of Lodiego, the type locality of *P. puberula,* has been lost (McVaugh, 1956), and it is not certain whether the site is in eastern Sinaloa or western Durango, there is no doubt that it is only a few miles from Cofradia, Sinaloa, the type locality of *P. scabra.*

REPRESENTATIVE SPECIMENS: **México.** DURANGO: Sierra Tres Picos, *Gentry 5282* (ARIZ, DS, F, GH, MO, NY, UC). SINALOA: Las Milpas, *Gentry 5361* (DS, GH, MO); Cofradia, *Gentry 5495* (ARIZ, DS, F, GH, MICH, MO, NY, UC, US); Badiraguato, *Gentry 5781* (ARIZ, DS, GH, MICH, MO, NY).

1e. **Pectis stenophylla** A. Gray var. **biaristata** (Rydb.) Keil, comb. nov. BASIONYM: *Pectis biaristata* Rydb., N. Am. Fl.**34:** 211. 1916. TYPE: **Mexico.** SINALOA: vicinity of Fuerte, *Rose, Standley & Russell 13537* (Holotype, NY!; isotype, UC!). Figure 2.

Plants annual. Stems 5–25 cm long, sparsely to densely hirtellous. Leaves linear to narrowly elliptic, 1–3 cm long, 1–3 mm wide, nearly glabrous to densely hirtellous, punctate marginally with brown oil glands or submarginally on the abaxial surface with black glands. Peduncles 3–5 cm long, glabrous to densely hirtellous. Heads broadly campanulate. Phyllaries linear to oblanceolate, 4–5 mm long, 1–2 mm broad, glabrous or hirtellous, punctate with small dark glands. Ray corollas 4.5–5 mm long. Disc corollas 17–26, ca 3 mm long. Achenes 2.3–2.5 mm long. Pappus of the rays 1.7–1.8 mm long; pappus of the disc 1–3 aristate or 10–20 setose, 1–2 mm long. Chromosome number: $n = 12$. Flowering September to March.

DISTRIBUTION: Southern Sonora (?) to central Sinaloa (Figure 3).

A collection from Sonora (*Sikes & Babcock 178*) is referred with some doubt to var. *biaristata.* It appears to be a mixed collection including some putative hybrids with another undetermined species. The plants resemble var. *biaristata,* but because of the depauperate nature of the specimens, the determination is made with some reservations.

REPRESENTATIVE SPECIMENS: **México.** SINALOA: W of Pericos, *Gentry 5751* (GH, MICH, MO); 16.8 mi SW of El Fuerte, *K & C 8752* (OS).

2. **Pectis rusbyi** Greene ex A. Gray, Syn. Fl. N. Am. **1**(2): 361. 1884. TYPE: **United States.** ARIZONA: Yavapai Co., Beaver Creek, *Rusby 317* (= *s.n.* or *655*) (Holotype, GH!; isotypes, F!, K!, MICH!, PH!, RSA!, UC!, US!). Figure 2.

Pectis palmeri S. Wats., Proc. Am. Acad. **24:** 58. 1889. TYPE: **Mexico.** SONORA: Guaymas, *Palmer 653* (Lectotype (here chosen), GH!).

Pectis mearnsii Rydb., N. Am. Fl. **34:** 209. 1916. TYPE: **United States.** ARIZONA: Yavapai Co., Fort Verde, *Mearns 184* (Holotype, NY!).

Strong-scented tap-rooted annuals, erect or branching from the base. Stems 5–50 cm long, erect or decumbent, often dichotomously branched, glabrous or sparsely puberulent on the angles. Leaves linear to narrowly elliptic, 1–5 cm long, 1–5 mm broad, often revolute, ciliate with 1–3 pairs of basal bristles 1–2 mm long, otherwise entire, glabrous or glabrescent, marginally punctate with rounded oil glands 0.2–0.7 mm diameter. Peduncles 2–8 cm long, glabrous, with 3–6 lance-attenuate or setiform bracteoles 1–3 mm long. Heads in forks of stems and axillary, becoming crowded in age. Phyllaries 8, oblong or narrowly obovate, 4–7 mm long, 1–2 mm broad, very obtuse to subacute, longitudinally striate with 3–5 usually conspicuous nerves on each side of the conspicuous, corky, basally gibbous midrib, hyaline margined, apically ciliolate, otherwise glabrous, punctate with 0–2 subterminal oil glands and 2–4 pairs of inconspicuous, rounded to narrow-elongated submarginal glands. Ray florets 8; corollas 5–11 mm long, with broadly ovate glabrous ligules and slender, glandular-puberulent tubes. Disc florets (7–) 20–55; corollas 3.5–5 mm long, bilabiate with the narrow lobe ca. twice the length of the teeth on the broad lobe, glandular-puberulent on the tube below. Achenes 3–4.5 mm long, strigillose or pilosulose. Pappus of the ray achenes 0–4 aristate and/or coroniform; awns slender, 1–4 mm

long, antrorsely barbed towards the tips. Pappus of the disc achenes coroniform or 15–30 setose; bristles 2.5–5 mm long, antrorsely barbed. Chromosome number: $n = 12$. Flowering August to February.

DISTRIBUTION: Central Arizona to southern Baja California and northern Sinaloa at elevations of 0–1200 meters (Figure 3).

Pectis rusbyi has a mostly Sonoran Desert distribution, barely extending beyond the desert into the grassland in central Arizona and occurring sporadically in the thorn forest of southern Sonora and northern Sinaloa.

In central Arizona, *Pectis rusbyi* exhibits a striking dimorphism of pappus structure. The type of *P. rusbyi* is essentially epappose, whereas the type specimen of *P. mearnsii,* collected only a few miles from that of *P. rusbyi,* has a setose pappus. However, based upon personal field observations, both pappus forms may coexist in the same population. For example, in both Maricopa and Yavapai Counties of Arizona, some individuals were found with a setose pappus and numerous others with only a coroniform pappus (*Keil 8569, 8575*). As a result of these observations, I regard both *P. rusbyi* and *P. mearnsii* as conspecific.

Kearney and Peebles (1942) placed *Pectis mearnsii* in synonymy with *P. palmeri,* a decision with which I heartily concur. The two taxa are essentially indistinguishable. However, with the present evidence of the conspecificity of *P. mearnsii* and *P. rusbyi, P. palmeri* must necessarily also be treated as a synonym of *P. rusbyi.*

In lowland areas of southern Sonora, a weedy, large-headed race occurs commonly along roadsides and in cultivated areas (*Keil & Canne 8632, 8652*). On some sites, this form is so common that it becomes an aspect dominant, coloring large areas with its showy yellow heads. In less disturbed sites, this form grades into the smaller-headed forms more typical of the species. Large-headed forms occur throughout much of the range of the species and are not limited to the weedy race. On the basis of the evidence presently available, taxonomic recognition of these forms does not seem justified.

Pectis rusbyi usually can be distinguished from other related species by its broad, apically flattened, longitudinally striate phyllaries. A few populations from Baja California and Sinaloa

(e.g. *Flyr 68, Wiggins 15533A*) have smaller, more convex, less conspicuously striate phyllaries. However, in other respects these plants are so similar to other populations of *P. rusbyi* that taxonomic separation even at the varietal level does not seem warranted.

Pectis rusbyi sometimes hybridizes with *P. papposa* var. *papposa* and with *P. filipes* var. *filipes* in Sonora where complex hybrid swarms may develop locally. In Arizona, however, where *P. papposa* var. *papposa* and *P. rusbyi* have been observed to grow together, no hybrids have been found.

REPRESENTATIVE SPECIMENS: **México.** BAJA CALIFORNIA SUR: Purissima, *Brandegee s.n.* (GH, US); W of Los Dolores, *Wiggins 15533A* (MICH, TEX). SINALOA: near Topolobampo, *Flyr 69* (TEX, WIS); 1.8 mi E of San Blas, *K & C 8744* (OS). SONORA: Guaymas, *Gentry 4682* (F, GH, MICH, MO, PH, SD, US); 11 mi NW of Cd. Obregon Airport, *K & C 8652* (OS). **United States.** ARIZONA: Maricopa Co.: White Tank Mts., *K 8569, 8570* (OS); Yavapai Co.: 2.5 mi S of Beaver Creek Ranger Station, *K 8575* (OS).

3. **Pectis peruviana** Keil, sp. nov. Figure 4.
TYPE: **Peru.** CAJAMARCA: Canyon of the Río Marañon, opposite Balsas, *Hutchison & Wright 5414* (Holotype, UC!; isotypes, F!, US!).

Plantae perennes, graveolentes. Caules usque ad 15 cm longi, solitarii aut basaliter ramosi, super medium ramulosi, rubelli, puberuli. Folia linearia, 1.5–3 cm longa, 1–1.5 mm lata, glabra, in dimidio inferiore setis 2–4 mm longis ciliata, mucronata vel setifera, glandibus oleosis marginalibus 0.2 mm diametro punctata. Capitula terminalia axillariaque. Pedunculi exiles, 2–3 cm longi, bracteolis 4–7, setiferis, 1–2 mm longis, glanduloso-punctatis. Involucra anguste campanulata, phyllariis 8, uniserialibus, linearibus, 6 mm longis, 1 mm latis, acutis, costa gracili, basaliter gibbosa, suberoso-incrassata fere usque ad apicem, tenuimarginatis, ad apices ciliolatis, aliter glabris, glandibus oleosis anguste aut late ellipticis ad apicem et utroque costae dense punctatis. Flosculi radii 8, corollis 6–8 mm longis, citrinis aut rubrescentibus, glabris, ligula 3–5 mm longa 1–1.5 mm lata apice minute tridenticulata. Flosculi disci 10–12, corollis 5 mm longis, citrinis, glabris, paene regularibus, 5-dentatis, dentibus 1.5 mm longis, antheris 1.5 mm longis, basaliter sagittatis, ad apicem appendice minute emarginata. Achenia cylindrica, discorum 3.5–4 mm longa, radiorum 4.5 mm longa, brunnea aut nigra, trichomatibus brevibus badiis

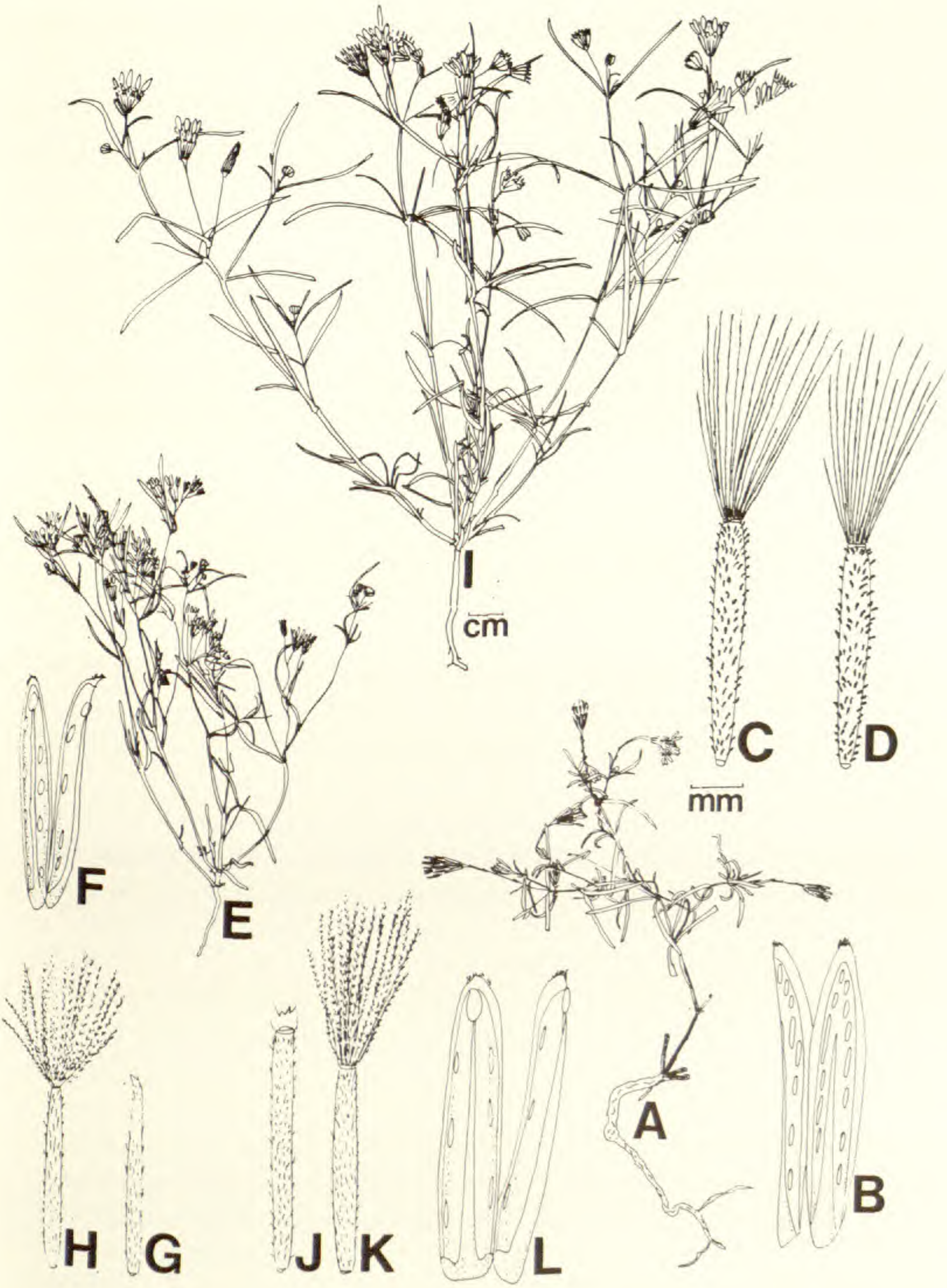


Figure 4. A-D, *Pectis peruviana* (*Hutchison & Wright 5414,* F); F-L, *Pectis papposa;* E-H, var. *papposa* (*Keil & Canne 8758,* OS); I-L, var. *grandis* (*Keil & McGill 7786,* OS). A, E, I, habit; B, F, L, phyllaries; C, G, J, ray achenes; D, H, K, disc achenes.

clavatis bicellularibus puberulenta. Pappus idem in flosculis radii ac disci, 12–20 setosus, setis 4 mm longis, antrorse scabridis. Chromosomatum numerus ignotus.

DISTRIBUTION: Presently known only from the type collection in northern Peru at an elevation of 1100 meters. *Pectis peruviana* is the only representative of sect. *Pectothrix* known to occur outside of North America. The occurrence of taxa in the North American deserts and also in Peru is not limited in *Pectis*, however, to sect. *Pectothrix*. *Pectis linifolia* L. of sect. *Pectidium* has races in the Sonoran Desert and also in the deserts of Peru. Indeed, Hutchison & Wright collected *P. linifolia* near the type locality of *P. peruviana*.

Pectis peruviana bears an overall resemblance to *P. stenophylla* var. *stenophylla*. Both are perennial taxa with narrowly linear leaves, elongate peduncles and a multisetose disc pappus. However, these taxa differ in several respects. *Pectis stenophylla* generally has smaller flowers, glandular puberulent rather than glabrous corollas, a biaristate rather than multisetose ray pappus and slender rather than clavate trichomes on the achenes.

The evolutionary relationship between *Pectis peruviana* and the remaining species of sect. *Pectothrix* is not certain. The multisetose pappus is apparently a primitive feature in *Pectis* and the aristate types have been derived from it. The perennial habit and multisetose pappus of *P. peruviana* suggest that this is a relatively primitive species in the section. If these assumptions are true, then *P. peruviana* is probably an early offshoot from the section *Pectothrix* progenitor and has been separated from the rest of the section for a considerable period of time. Whatever the length of time that *P. peruviana* has remained in isolation from the rest of the section, it apparently has not enjoyed the evolutionary success that the North American species have displayed.

4. **Pectis papposa** Harv. & Gray in A. Gray, Mem. Am. Acad. **4:** 62. 1849. TYPE: **Mexico.** "CALIFORNIA," (probably collected near Hermosillo or Guaymas, Sonora), *Coulter 331* (Holotype, TCD!; isotypes, GH!, K, two sheets!). Figure 4.

Pectis papposa Harv. & Gray var. *epapposa* A. Gray, Geol. Surv. Calif. Bot. **1:** 617. 1880. TYPE: **United States.** CALIFORNIA: San Diego Co., Larkens, *Palmer 200 p. p.* (Holotype, GH!).

Bushy strong-scented annuals. Stems 1–30 cm long, much branched, glabrous or minutely puberulent. Leaves linear, 1–6 cm long, 1–2 mm wide, basally ciliate with 1–3 pairs of bristles 1–2 mm long, otherwise entire, glabrous, marginally punctate with rounded to oval oil glands 0.3–0.5 mm diameter. Peduncles 3–40 mm long, glabrous, with 2–6 hyaline, lanceolate bracteoles ca. 1 mm long. Heads clustered at tips of branches. Involucre cylindric to campanulate. Phyllaries 8, rarely 7, 9 or 10, linear, 3–8 mm long, 0.5–1.7 mm wide, apically acutish, basally truncate, gibbous, strongly convex-keeled almost to the tips, narrowly hyaline-margined, apically ciliolate, otherwise glabrous, punctate with 1–5 swollen subapical glands and 2–5 pairs of smaller, inconspicuous submarginal glands, occasionally with additional dorsal glands. Ray florets 8, rarely 7, 9, or 10; corollas 3–8 mm long, with narrowly to broadly ovate glabrous ligules and slender glabrous or glandular-puberulent tubes. Disc florets 6–34; corollas 2–5.5 mm long, bilabiate, with the narrow lobe ca. twice the length of the teeth on the broad lobe, glabrous or glandular-puberulent below. Achenes 2–5.5 mm long, strigillose or pilosulose with slender, bulbous-tipped unicellular trichomes. Pappus of ray florets coroniform, ca. 0.2 mm long, rarely 1-several aristate or setose. Disc pappus 16–24 setose, 1.5–4 mm long, or occasionally only coroniform; bristles slender, sub-plumose, spreading. Chromosome number: $n = 12$.

DISTRIBUTION: Southern California and southwestern Utah to western Texas, south to Baja California, Sinaloa, Chihuahua and Coahuila (Figure 5). *Pectis papposa* occurs, often in great abundance, in all four of North America's deserts, occupying a variety of habitats. Under favorable conditions, this species sometimes becomes an aspect dominant, coloring wide areas with its bright yellow heads. *Pectis papposa* is divided into two well-marked geographic varieties. The typical one occurs in the Mojave and Sonoran Deserts, whereas var. *grandis* is restricted mostly to the Chihuahuan Desert.

4a. **Pectis papposa** Harv. & Gray in A. Gray, Mem. Am. Acad. **4:** 62. 1849. var. **papposa.** Figure 4.

Stems 1–20 cm long. Leaves 1–3 cm long, 1–2 mm broad. Peduncles 3–10 (–25) mm long, 3–6 bracteolate. Heads densely

clustered at tips of the branches, or in some Mexican forms more diffuse. Phyllaries 3–5 mm long, ca. 0.5 mm broad, punctate with 1–3 subapical glands and 2–3 pairs of submarginal glands. Ray corollas 3–6 mm long, ca. 0.5 mm broad, glabrous or glandular-puberulent. Disc florets 6–14 (–18); corollas 2–3.5 (–4) mm long, glabrous or glandular-puberulent. Achenes 2–4.5 mm long. Pappus of disc achenes setose or sometimes coroniform; bristles 1–2.5 mm long. Chromosome number: $n = 12$. Flowering mostly June to December.

DISTRIBUTION: Southern California and southwestern Utah to southwestern New Mexico, south to Baja California and central Sinaloa at elevations ranging from minus 60 to 1500 meters (Figure 5).

Pectis papposa var. *papposa* often colors large areas of the Sonoran Desert during late summer. It is particularly abundant in central Arizona on the broad inter-mountain alluvial plains and also occurs on the low desert mountain ranges. The plants of var. *papposa* are morphologically variable, and a number of intergrading local races occur within its range. Peduncle length, branching habit, and pappus structure are among the features that vary, but none of these populational differences seems worthy of formal taxonomic recognition.

Bradley and Haagen-Smit (1949) reported that a large portion of the essential oils of *Pectis papposa* (var. *papposa*) is composed of cumin, and they suggested that *P. papposa* might be grown as a commercial crop for this oil. To my knowledge, this suggestion apparently has not been pursued.

REPRESENTATIVE SPECIMENS: **México.** BAJA CALIFORNIA: S of Laguna Seca Chapala, *Carter, Alexander & Kellogg 1890* (DS, GH, MO, SD); Los Angeles Bay, *Palmer 657* (GH, ND-G, NY, UC, US). BAJA CALIFORNIA SUR: 6 mi S of La Paz, *Hammerly 235* (CAS, DS, SD). SINALOA: 1 mi E of Altata, *Flyr 113* (TEX, WIS). SONORA: Corral, *Gentry 4745* (DS, GH, MICH, MO); near Gulf of California, *Pringle s.n.* (F, MICH, PH, WIS).

United States. ARIZONA: Mohave Co.: Willow Springs, *Demaree 41527* (ASC, ASU, GH, KANU, SMU); Pinal Co.: Maricopa, *Pringle, s.n.* (F, GH, MO, PH). CALIFORNIA: Riverside Co.: La Quinta, *Rose 61063* (CAS, ENCB, TEX); San Bernardino Co.: Needles, *Jones 3872* (CAS, DS, F, PH). NEVADA: Clark Co.: Charleston Mts., *Clokey 8197* (CAS, DS, F, GH, KSC, MICH, MIL, MO, PH, SD, SMU, TEX, WIS); Lincoln Co.: Timpahute Range, *Reveal & Holmgren 1904* (DS, KANU, KSC, MICH, SMU, TEX). NEW MEXICO: Hidalgo Co.: Cienega Lake turnoff on US 80, *K & M 8500* (OS). UTAH: Washington Co.: 8.6 mi N of St. George, *Gould 1363* (CAS, F, GH, ND, PH, RSA).

4b. **Pectis papposa** Harv. & Gray in A. Gray var. **grandis** Keil, Brittonia **26:** 32. 1974. TYPE: **United States.** TEXAS: Presidio Co., 3 mi E of junct US Rte 67 on Texas Rte 170, E of Presidio, *McGill & Keil 7768* (Holotype, US!; isotypes, ARIZ!, ASU!, ENCB!, F!, GH!, MICH!, MO!, NY!, OS!, RSA!, SMU!, TEX!, UC!). Figure 4.

Stems 5–30 cm long. Leaves 2–6 cm long, 1–2 mm broad. Peduncles 1–4 cm long, 2–6 bracteolate. Heads usually several at tips of branches. Phyllaries 5–8 mm long, 1–1.7 mm broad, punctate with 1–5 subterminal glands and 2–5 pairs of submarginal glands. Ray corollas 5–8 mm long, glabrous or sparsely glandular-puberulent. Disc florets 12–24 (–34); corollas 3–5 mm long, glabrous or glandular-puberulent. Achenes 3–5.5 mm long. Pappus of disc achenes 2.5–4 mm long, setose or rarely short-coroniform. Chromosome number: $n = 12$. Flowering June to October.

DISTRIBUTION: Southern New Mexico and southwestern Texas to Chihuahua and northern Coahuila; disjunct in Arizona and northeastern New Mexico (Figure 5). The distribution of this variety is primarily in the Chihuahuan Desert at elevations of 1000 to 2000 meters. The plants of var. *grandis* are particularly common in the Rio Grande valley in Texas, New Mexico and northern Mexico. This taxon is undoubtedly more common in northern Coahuila than is indicated by presently available collections. The plants grow almost to water's edge along the Rio Grande on the Texas side of the border, but I have seen no collections from the opposite bank.

REPRESENTATIVE SPECIMENS: See Keil (1974) for specimen citations for *Pectis papposa* var. *grandis*.

5. **Pectis angustifolia** Torrey, Ann. Lyceum Nat. Hist. New York **2:** 214. 1828. TYPE: **United States.** (COLORADO or NEW MEXICO): "on the Rocky Mountains," 1820, *James s.n.* (Holotype, NY!). Figure 6.

Helioreos angustifolius (Torrey) Raf., Atlantic Jour. **1:** 145. 1832.

Pectidopsis angustifolia (Torrey) DC., Prodr. **5:** 98. 1836, nom. illeg.

Pectis angustifolia Torrey var. *subaristata* A. Gray, Smithsonian Contr. Knowl. **3:** 82. 1852. TYPE: **United States.** TEXAS: "valley between the Pecos and the Limpia," *Wright 244* (Holotype, GH!; isotypes, K!, MO!, NY!, US!).

Pectis papposa Harv. & Gray in A. Gray var. *sessilis* M. E. Jones, Contr. West. Bot. **12:** 46. 1908. TYPE: **United States.** NEW MEXICO: Socorro Co., Socorro, *Diehl s.n.* (Lectotype (*fide* Blake, 1945), POM!; photo and fragment of lectotype, US!).

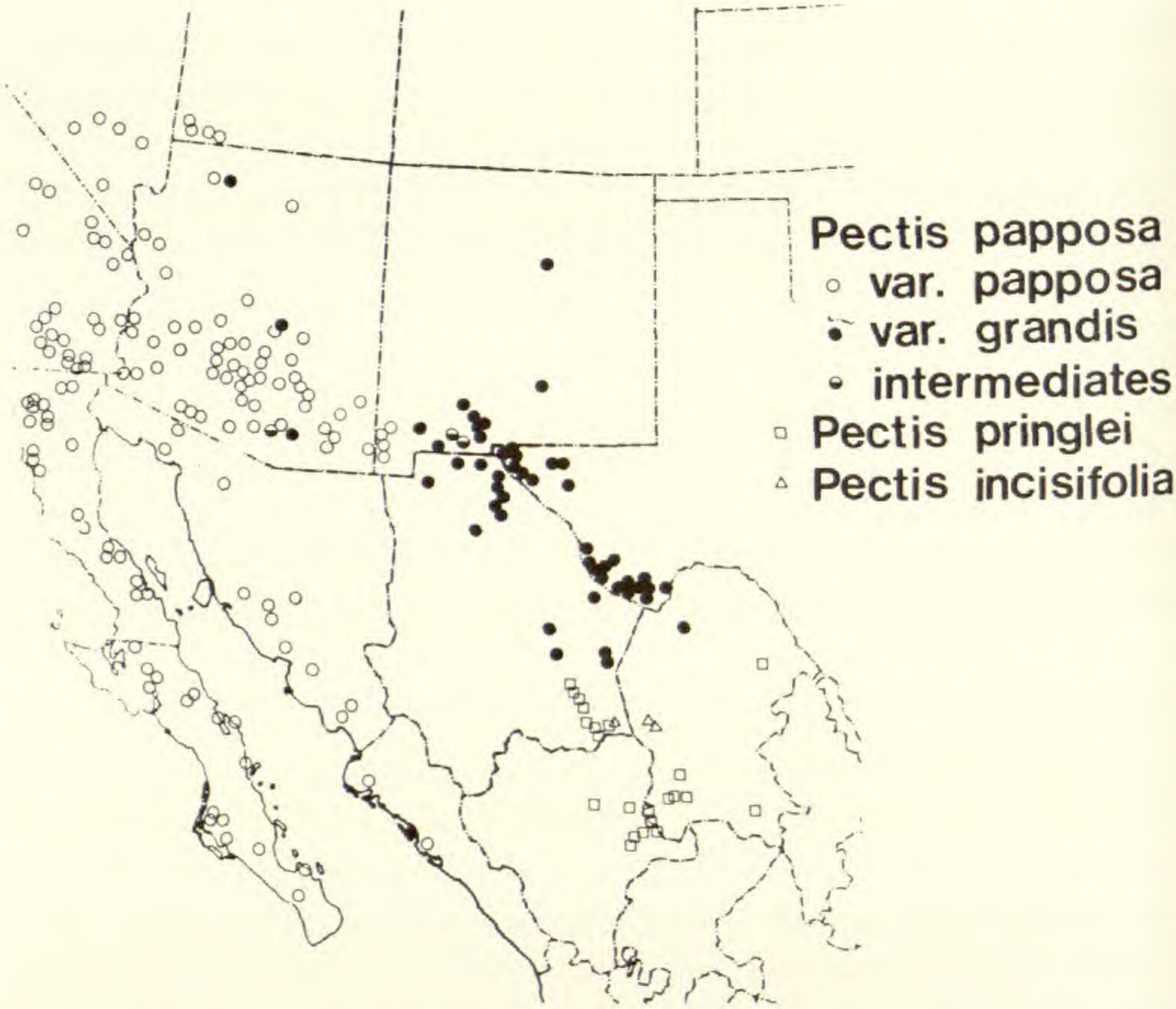


Figure 5. Geographical distribution of *Pectis papposa, P. pringlei* and *P. incisifolia.*

Annual or perennial herbs from a slender tap-root or ligneous caudex. Stems 1–20 cm long, usually branched from the base, glabrous or minutely puberulent. Leaves linear, 1–4.5 cm long, 1–3 mm broad, 2–5 ciliate at the base with bristles 1–2 mm long, mucronate, often strongly revolute, glabrous, marginally punctate with glands 0.2–0.7 mm diameter. Peduncles 1–20 mm long, with 2–5 bracteoles 1–3 mm long. Heads congested at ends of branches, narrowly campanulate or cylindrical. Phyllaries linear or narrowly oblanceolate, 2.5–5.5 mm long, obtuse, basally truncate and strongly gibbous, very strongly convex-keeled nearly to the apex, glabrous, punctate subterminally with 1 or 2 swollen oil glands, and submarginally with 2–5 pairs of smaller glands. Ray florets 8; corollas 3–5 (–7) mm long, glandular-puberulent or nearly glabrous. Disc florets (7–) 10–20; corollas 2.5–3.5 mm long, regular or bilabiate, glandular-puberulent. Achenes 2.5–4 mm long, stri-

gillose with bifurcate trichomes. Pappus variable, coroniform and/or 1–7 aristate or setose, 1–2 mm long. Chromosome number: $n = 12$.

DISTRIBUTION: Wyoming and Nebraska south to Durango, San Luis Potosí and Veracruz (Figure 7).

In the *Pectis angustifolia* complex previous workers (Gray, 1884; Fernald, 1897; Rydberg, 1916) have relied primarily on the features of the pappus as taxonomic characters. Three taxa traditionally have been recognized in the complex on the basis of differences in pappus structure: *Pectis angustifolia, P. angustifolia* var. *subaristata* and *P. tenella.* A fourth group of plants has twice been named as a species (*P. fastigiata* Gray, 1849; *P. texana* Cory, 1937) and twice re-united with *P. angustifolia* (Gray, 1852; Correll & Johnston, 1970).

The value of the pappus as a character in this complex has been greatly overemphasized. Although easily distinguishable forms exist in some regions, in other areas there is so much variation in pappus structure that as many as three "taxa" could be recognized from the members of an otherwise homogeneous population. A re-examination of taxonomic boundaries, necessitated by the breakdown of the traditionally accepted scheme, has led me to two conclusions. First, the *Pectis angustifolia* complex should be recognized as a single species with three varieties: *P. angustifolia* var. *angustifolia,* var. *tenella* and var. *fastigiata.* Second, Gray's var. *subaristata* has often been misapplied, and in its strict interpretation, cannot be distinguished from var. *angustifolia.*

5a. **Pectis angustifolia** Torrey, Ann. Lyceum Nat. Hist. New York 2: 214. 1828. var. **angustifolia.** Figure 6.

Bushy lemon-scented annuals. Stems 1–20 cm long, densely leafy at the tips. Leaves 1–4.5 cm long, 1–3 mm wide, conspicuously flared at the bases. Peduncles mostly 1–10 mm long, 1–4 bracteolate, often wholly or partially concealed by the bases of the subtending leaves. Phyllaries 2.5–5.5 mm long, linear, strongly keeled to the tips, abruptly truncate, punctate with 1 or 2 subterminal glands 0.2–0.5 mm long, and smaller submarginal glands. Ray corollas 3–5 mm long. Disc florets (7–) 10–20; corollas 2.5–3.5 mm long, slightly bilabiate. Achenes 2.5–4 mm long.

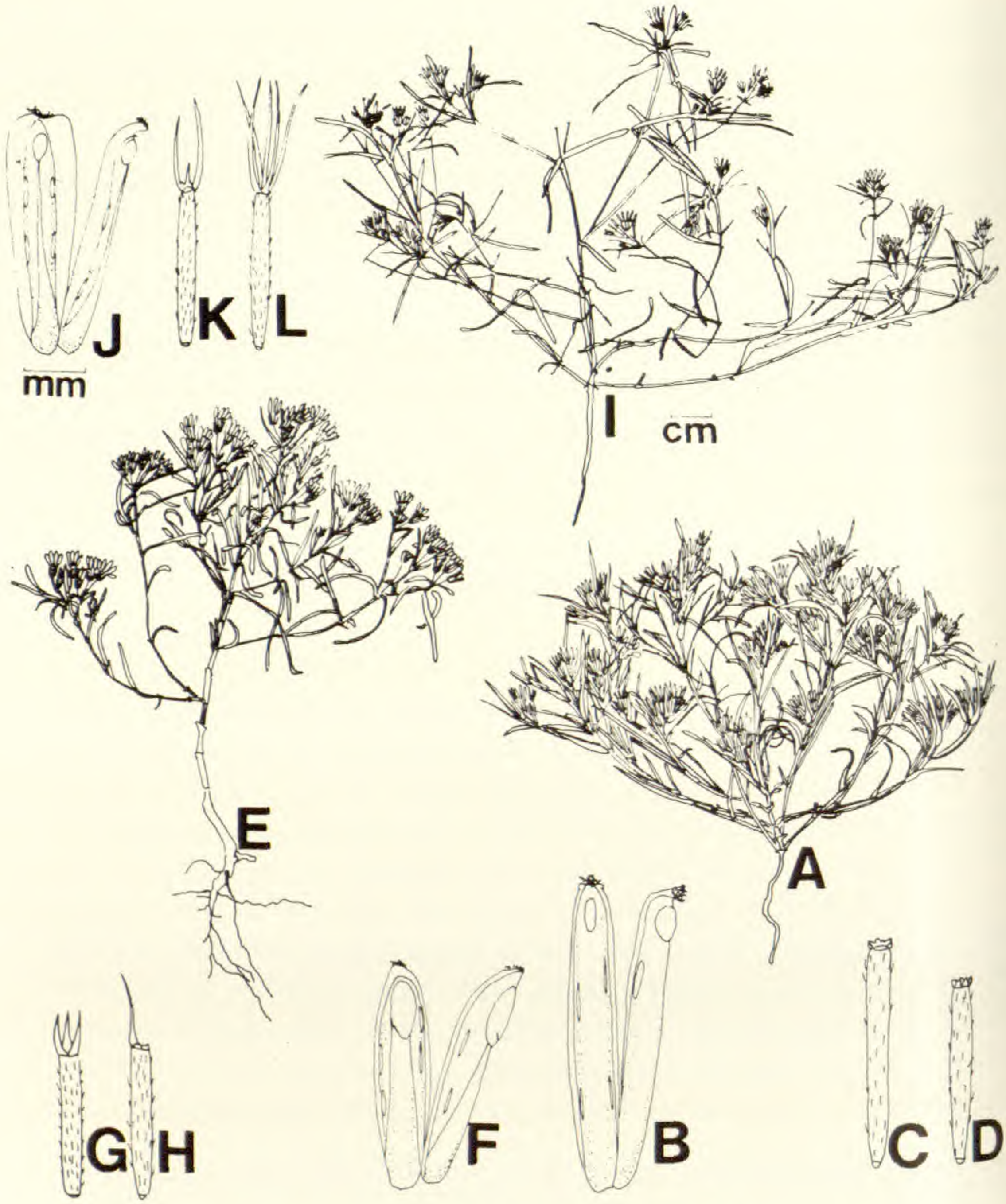


Figure 6. *Pectis angustifolia;* A-D, var. *angustifolia* (*Keil 7634*,OS); E-H, var. *fastigiata* (*Tharp & Warnock 45-30,* ARIZ); I-L, var. *tenella* (*Keil & McGill 7849,* OS). A, E, I, habit; B, F, J, phyllaries; C, H, K, ray achenes; D, G, L, disc achenes.

Pappus coroniform, 0.1–0.3 mm long, or in some Texas and Chihuahua populations also 1–7 aristate or setose. Chromosome number: $n = 12$. Flowering July to October.

DISTRIBUTION: Western Nebraska to eastern Arizona, western Texas, Chihuahua and northern Durango, grading into var. *tenella* in eastern Chihuahua and Durango (Figure 7).

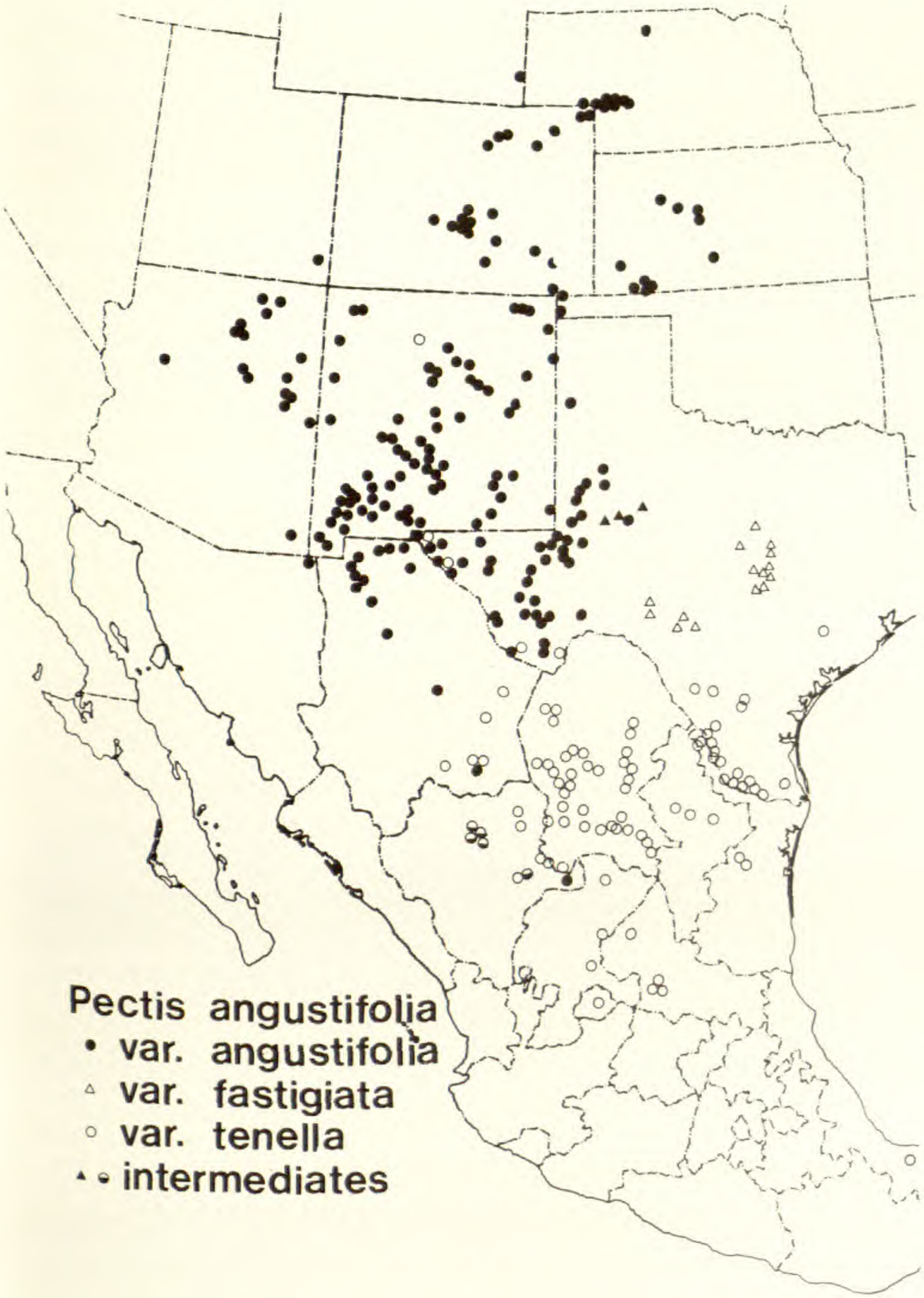


Figure 7. Geographical distribution of *Pectis angustifolia.*

The present interpretation of morpho-geographical variation in the *Pectis angustifolia* complex has necessitated a re-interpretation of var. *subaristata.* This name has been applied widely over the years to any individual with a few-bristled pappus. An examination of the type material of this taxon revealed that, with the exception of the slightly bristly pappus, these plants are not distinguishable from individuals of var. *angustifolia.*

The "subaristate" forms to which this name has been applied are of several different origins. Spontaneous "subaristate" variants occur sporadically through much of the range of *Pectis angustifolia* var. *angustifolia* and are particularly common in western Texas and northern Mexico. Within populations of var. *tenella,* individuals may be "subaristate" or even completely epappose. A similar condition sometimes occurs in var. *fastigiata.* In some areas of northern Mexico, individuals intermediate between var. *angustifolia* and var. *tenella* may have a subaristate pappus. Finally, in eastern Chihuahua and western Texas, "subaristate" races have developed apparently as a result of hybridization and introgression between var. *angustifolia* and *P. papposa* var. *grandis.*

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: near Chihuahua, *Pringle 648* (DS, F, GH, MICH, MO, NY, PH, RSA, US); 43 mi N of Villa Ahumada, *Stuessy 1114* (DS, ENCB, NY, TEX). DURANGO: 1.8 mi E of Nazareno, *K & M 8014* (OS). SONORA: Guadelupe Canyon, *Mearns & Merton 2034* (DS, NY, US).

United States. ARIZONA: Coconino Co.: 12 mi N or Cameron, *Cutler 3122* (DS, GH, MO, NY, US); Holbrook, *Zuck s.n.* (MO, NY, US). COLORADO: Fremont Co.: Royal Gorge, *Ownbey 1508* (DS, GH, MO, NY, UC); Otero Co.: 15 mi NE of La Junta, *Rollins 1873* (DS, MO, ND, NY, US). KANSAS: Ellis Co.: 12 mi SW of Hays, *Runyon & Bondy 288* (MO, PH, SMU); Trego Co.: without locality, *Hitchcock 294* (GH, KSC, MO, NMC, NY). NEBRASKA: Cherry Co.: Ft. Niobrara, *Bates s.n.* (CAS, GH); Deuel Co.: Big Springs Rd. at S. Platte River, *K 7633* (OS). NEW MEXICO: Dona Ana Co.: Organ Mts., *Wooton 426* (DS, GH, KSC, MO, ND-G, NMC, NY, POM, UC, US); Grant Co.: Bear Mts., *Metcalfe 699* (ARIZ, GH, MO, NMC, NY, POM, UC, US); Lincoln Co.: Gray, *Skehan 45* (F, GH, KSC, MO, NMC, NY, POM, UC, US); Sierra Co.: Berendo Creek, Black Range, *Metcalfe 1387* (CAS, F, GH, MO, NMC, NY, POM, UC, US). OKLAHOMA: Cimarron Co.: 2 mi S of Kenton, *Demaree 13381* (GH, MO, NY, PH, POM, SMU). TEXAS: Deaf Smith Co.: 1 mi S of Glenrio, *Waller 1526* (ASU, ENCB, SMU, TTC); Jeff Davis Co.: Ft. Davis, *Palmer 32151* (MO, PH). UTAH: San Juan Co.: Copper Canyon, *Cutler 3146* (GH, MO, NY, SMU). WYOMING: Goshen Co.: 12 mi below Ft. Laramie on N. Platte, *Simpson's Exped. s.n.* (MO)

5b. **Pectis angustifolia** Torrey var. **tenella** (DC.) Keil, comb. nov. BASIONYM: *Pectis tenella* DC., Prodr. **5:** 99. 1836. TYPE:

Mexico. TAMAULIPAS: "prope Laraedo," *Berlandier 2009* (= 599) (Holotype, G-DC; photo of holotype, US!; microfiche, IDC 800. 787: III. 5!; isotypes, (*2009*) GH!, MO!, NY!, US!, (*599*) GH!, K!, MO!, PH!). Figure 6.

Bushy strong scented annuals. Stems 2–15 cm long. Leaves 1–4 cm long, not or scarcely flared at the base, evenly distributed on the stems. Peduncles 5–15 mm long, 1–4 bracteolate, not or scarcely concealed by the bases of the subtending leaves, the heads evidently slender-peduncled. Phyllaries 3–5 mm long, linear, widest near the middle, punctate with a solitary subterminal gland 0.2–0.5 mm long, and smaller submarginal glands. Ray corollas 3–5 mm long. Disc florets 10–18; corollas 2.5–3.5 mm long, regular or slightly bilabiate. Achenes 2.5–4 mm long. Pappus highly variable, coroniform and/or 1–7 setose or aristate, 1–3 mm long. Chromosome number: $n = 12$. Flowering June to January.

DISTRIBUTION: Eastern Chihuahua and southern Texas to Aguascalientes, San Luis Potosí and Veracruz. Also one station in northern New Mexico where probably adventive (Figure 7).

In most areas, *Pectis angustifolia* var. *tenella* is easily distinguished from var. *angustifolia.* Some individuals from Chihuahua, Durango, Aguascalientes and Zacatecas, however, possess the flared leaf bases or lemon scent of var. *angustifolia,* but in most other respects they resemble var. *tenella.* Because these individuals have the open branching pattern and bristly pappus of var. *tenella,* they are referred to this variety in the present treatment.

REPRESENTATIVE SPECIMENS: **México.** AGUASCALIENTES: near Aguascalientes, *Rose & Hay 7753* (GH, NY, US). CHIHUAHUA: 27 mi E of Jiménez, *Shreve 8867* (ARIZ, GH, MICH, US). COAHUILA: 27 mi S of Monclova, *K & M 7879* (OS); 25 mi SW of Sabinas, *Wynd & Muller 215* (ARIZ, GH, MO, ND, NY, US). DURANGO: between Yerbanis & Cuencamé, *Gentry 6941* (GH, MICH, US); 25 mi N of Bermejillo, *K & M 8192* (OS). NUEVO LEÓN: 25 km NE of Monterrey, *Dieterle 3678* (MICH). SAN LUIS POTOSÍ: San Luis Potosí, *Shaffner 325 [=235, 751]* (F, GH, MICH, NY, UC, US). TAMAULIPAS: Mier, *Gregg s.n.* (GH, MO, PH); vicinity of Victoria, *Palmer 431* (F, MO, NY, UC, US). VERACRUZ: Chinameca, *Peniche 27* (F, US). ZACATECAS: near San Raphael, *Shreve 9390* (ARIZ).

United States. NEW MEXICO: Rio Arriba Co.: Capulin Volcano, *Clark 4608* (UNM). TEXAS: McMullen Co.: 11¼ mi S of Tilden, *Cory 55339* (SMU, US); Webb Co.: without locality, *Tharp s.n.* (GH, MO, TEX, UC).

5c. **Pectis angustifolia** Torrey var. **fastigiata** (A. Gray) Keil, comb. nov. BASIONYM: *Pectis fastigiata* A. Gray, Mem. Am. Acad. **4:** 62. 1849. TYPE: **United States.** TEXAS: Travis Co., Austin, *Wright s.n.* (Holotype, GH!; isotypes, GH!, NY!, US!). Figure 6.

Pectis texana Cory, Rhodora **39:** 421. 1937. TYPE: **United States.** TEXAS: Sutton Co., Ranch Experiment Station, *Cory 15382* (Holotype, GH!; isotype, TEX!).

Fibrous-rooted strong-scented perennials or sometimes annuals. Stems 5–15 cm long, sometimes woody at the base. Leaves 1–4 cm long, 1–2 mm wide, not or scarcely flared at the base, not crowded at the tips of the branches. Peduncles 3–30 mm long, 3–6 bracteolate. Phyllaries 2.5–4.5 mm long, narrowly oblanceolate, punctate with a conspicuous subterminal oil gland 0.5–1 mm long and 1 or 2 pairs of smaller submarginal glands. Ray corollas 4–6 mm long. Disc florets 8–21; corollas regular, 2.7–4 mm long. Achenes 2.5–3.5 mm long. Pappus 0–4 aristate, 0.5–1 (–2) mm long, also more-or-less coroniform. Chromosome number: $n = 12$. Flowering September to November.

DISTRIBUTION: Endemic to the Edwards Plateau area of central Texas, mostly on limestone soils (Figure 7).

Until now, the perennial nature of some plants of *Pectis angustifolia* var. *fastigiata* has not been noted. Some individuals of this taxon develop strongly lignified root crowns. Although both *P. fastigiata* and *P. texana* were both described as annuals, it is apparent from examination of additional specimens of these plants that the perennial condition prevails in several populations.

Correll and Johnston (1970) evidently were referring primarily to populations of var. *fastigiata* when they indicated that, in Texas, *Pectis angustifolia* occurs primarily on limestone soils. Both var. *angustifolia* and var. *tenella* occur commonly on a variety of substrates and are common on sandy soils. Only var. *fastigiata* is largely restricted to limestone soils.

In west-central Texas, on the western edge of the Edwards Plateau, several populations occur which are somewhat similar morphologically to *Pectis angustifolia* var. *tenella* (*Tracy 1852; Eggert s.n.*, 13 Jun 1900). These sites, however, are well outside the general range of this variety. The populations are situated within the range of var. *angustifolia* however, and not far outside the range

of var. *fastigiata.* Although none of these plants appear to have the perennial habit of var. *fastigiata,* some individuals possess the elongated subterminal oil glands of the phyllaries and the short aristate pappus of this variety as well as the flared leaf bases of var. *angustifolia.* Because of their geographical location and the evidence of morphological intermediacy, it seems best to treat these populations as intermediates between var. *angustifolia* and var. *fastigiata* rather than as disjunct populations of var. *tenella.*

REPRESENTATIVE SPECIMENS: **United States.** TEXAS: Bell Co.: 10 mi W of Belton, *Tharp s.n.* (GH, MO, NY, SMU, TEX, UC); Travis Co.: near Jollyville, *Tharp & Warnock 45–30* (ARIZ, DS, KSC, MICH, MO, NY, PH, RSA, SMU, TEX, TTC, US, WIS).

6. **Pectis pringlei** Fern., Proc. Am. Acad. **33:** 76. 1897. TYPE: **Mexico.** COAHUILA: Jimulco, *Pringle 125* (Holotype, GH!). Figure 8.

Strong-scented, tap-rooted annuals, branching from the base. Stems 2–25 cm long, erect or decumbent, pseudodichotomously branched, glabrous or puberulent. Leaves linear, 1–5 cm long, 1–2 mm broad, often revolute, basally ciliate with 2–4 pairs of bristles 1–2 mm long, glabrous or abaxially puberulent, marginally punctate with conspicuous elliptic to round oil glands 0.2–0.7 mm diameter. Peduncles 8–50 mm long, glabrous, with 1–4 scattered lanceolate bracteoles 1–2 mm long. Heads in forks of stems and axillary, becoming somewhat crowded in age. Phyllaries 8, linear to narrowly oblong, 4–6.5 mm long, 1–1.5 mm broad, obtuse, conspicuously hyaline-margined, with slender, corky, basally gibbous midribs, apically villous-ciliolate, otherwise glabrous, each punctate with a solitary subterminal oil gland and 1–4 pairs of smaller, elongated submarginal glands. Ray florets 8; corollas 5.5–6 mm long, with narrowly to broadly obovate glabrous ligules and sparsely glandular-puberulent tubes. Disc florets 10–21; corollas 3–4 mm long, regular, glandular-puberulent. Achenes 3–4.5 mm long, strigillose. Pappus 1–4 aristate; awns slender, antrorsely barbed, 2–4 mm long. Chromosome number: $n = 12$. Flowering July to November.

DISTRIBUTION: Southern Chihuahua, southern Coahuila and northern Durango at 1100 to 1800 meters elevation (Figure 5).

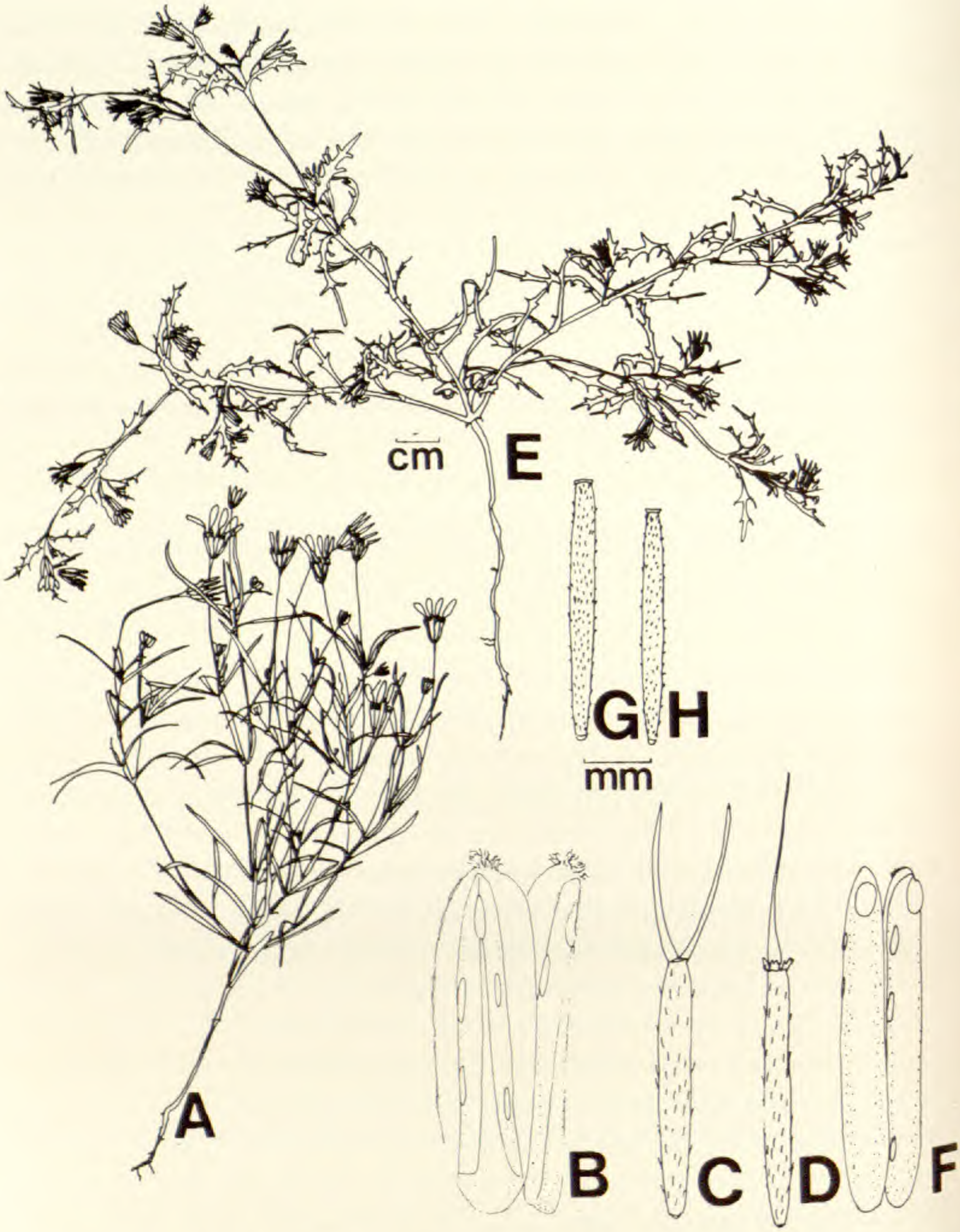


Figure 8. A-D, *Pectis pringlei* (*Keil & McGill 7976*, OS); E-H, *Pectis incisifolia* (*Keil & McGill 8105*, OS). A, E, habit; B, F, phyllaries, D, G, ray achenes; C, H, disc achenes.

Pectis pringlei is locally quite common on dry stony sites in the southern parts of the Chihuahuan Desert. Unlike the more widespread *P. angustifolia*, *P. pringlei* usually does not occupy sites on

the broad alluvial plains of this region. The latter species occurs on a variety of substrates including both igneous and sedimentary rocks.

Extreme forms of *Pectis pringlei* approach *P. papposa* var. *grandis* in habit and general aspect. The two taxa are easily distinguishable by their very different pappus structure and by the morphology of their phyllaries (Figures 4, 8). Some small, rather depauperate individuals of *P. pringlei,* on the other hand, resemble *P. angustifolia* var. *tenella.* The overall size and less congested appearance of the heads on *P. pringlei,* however, make distinguishing the two taxa rather easy. I have observed *P. pringlei* growing with both *P. papposa* var. *grandis* and with *P. angustifolia* var. *tenella* without any evidence of hybridization. The similarities observed with these taxa have probably resulted from localized selection rather than from hybridization and introgression.

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 48 km S of Jiménez, *Cronquist & Fay 10759* (MICH, NY, OS); 19.5 mi S of Cd. Camargo, *K & M 8251* (OS). COAHUILA: jctn. of rd. to San Pedro & Rte. 40, *K & M 7988* (OS); 10.3 mi S of Rancho los Charcos, *K & M 8164* (OS); Jimulco, *Pringle 10091* (ARIZ, ASU, CAS, F, GH, LL, MICH, MO, NY, PH, SMU, UC, US). DURANGO: 17.5–22 mi SW of Nazareno, *K & M 8033, 8038, 8041* (OS); Huarichic, *Pennell 18603* (MICH, NY, PH).

7. **Pectis incisifolia** I. M. Johnst., Jour. Arnold Arb. **21:** 75. 1940. TYPE: **Mexico.** COAHUILA: just S of Laguna del Rey, *Johnston 7824* (Holotype, GH!; isotypes, CAS!, LL!, US!). Figure 8.

Strong-scented taprooted annuals. Stems decumbent to prostrate, dichotomously branched, 5–40 cm long, glabrous, stramineous to red-purple. Leaves linear to elliptic in outline, 1–4 cm long, 2–15 mm wide, irregularly pinnatifid with 2–4 pairs of remote, linear to triangular, acute, mucronate or bristle-tipped lobes 1–5 mm long and 1–2 mm wide, basally incised-ciliate with 2–4 pairs of slender bristle-tipped teeth 1–2 mm long, glabrous on both surfaces, marginally punctate with rounded oil glands 0.2–0.4 mm diameter. Peduncles 5–10 mm long, glabrous, with 1–3 linear-acute bracteoles to 2.5 mm long. Heads solitary in the forks of the stem, cylindric or campanulate. Phyllaries 8, narrowly linear, 5–6 mm long, 0.5-0.7 mm wide, strongly convex-keeled, basally gibbous, very narrowly scarious-margined, apically narrowed and subacutish, tipped with a tuft of minute hairs,

otherwise glabrous, each punctate with a solitary rounded subterminal oil gland ca 0.5 mm diameter and 1–4 pairs of slender, inconspicuous submarginal glands. Ray florets 8; corollas 4–6 mm long, with narrowly to broadly obovate ligules 2–4 mm long, glandular-puberulent on the tubes. Disc florets 12–15; corollas 3–4 mm long, regular, with teeth ca. 1 mm long, glandular-puberulent on the tube and throat. Achenes 3.5–5 mm long, glandular puberulent. Pappus absent. Chromosome number: $n = 12$. Flowering August to October.

DISTRIBUTION: Very local in southeastern Chihuahua and west-central Coahuila on sand dunes. Chihuahuan Desert endemic (Figure 5).

Pectis incisifolia appears to have a relict distribution. This species occurs only on the sand dunes which border certain playas or lagunas in the interior of the Chihuahuan Desert. *Pectis incisifolia* may have occupied a wider range before post-Pleistocene drought brought about the formation of the large playas. As noted by Johnston (1940), these areas are remarkable for the endemism of their floras.

Pectis incisifolia is a very distinctive species, well differentiated from all other species in sect. *Pectothrix* by its prostrate habit, pinnatifid leaves, and glandular, completely epappose achenes. This taxon does not appear to be closely related to any of the other species. Johnston (1940) suggested that *P. incisifolia* might be most closely related to *P. angustifolia.* Although I cannot rule out that possibility, I feel that a closer relative might be *P. papposa* because of similarities in the phyllary morphology. However, any relationship of *P. incisifolia* to either of these species is distant.

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 9 km NE of Carillo toward Guimbalete, *Chiang, Wendt & Johnston 9052* (LL); 36 mi ENE of Escalón along trail to Esmerelda, *Henrickson 7766* (LL); 5 mi NE of Laguna Palomas, *Johnston 7827* (GH); 5 mi E of Carillo, *Muller 3317* (GH, LL, MICH, UC). COAHUILA: ½mi E of Salinas on rd. crossing lake bed leading to La Chemica, *Bacon & Leverich 1221* (TEX); S of Laguna del Rey, *K & M 8101, 8102A, 8105, 8109, 8117, 8120* (OS); 6 mi N of Noria near Laguna del Rey, *Shreve 8844* (ARIZ, US).

8. **Pectis purpurea** Brandeg., Zoe **5:** 225. 1905. TYPE: **Mexico.** SINALOA: Cofradia, *Brandegee s.n.* (Holotype, UC!; isotype, GH!). Figure 9.

Plants annual. Stems 15–50 cm tall, one to several from the base, erect or ascending, branching above. Leaves 1.5–6 cm long, 1–9 mm wide, linear to narrowly elliptic or lanceolate, sometimes strongly revolute, punctate on the undersurface with circular or elliptic oil glands. Peduncles 4–13 cm long, with 4–10 bracteoles, these 1.5–3 mm long, scale-like, linear to lanceolate, hyaline except for the darkened midribs, marginally ciliolate, often punctate with 1–2 glands. Heads solitary, terminal or axillary, campanulate. Phyllaries 8 or 9, 4–6.5 mm long, narrowly to broadly angular-obovate, obtuse to acute, with thin, hyaline margins and rounded backs, obtusely keeled below and basally gibbous, punctate with scattered linear to ovate oil glands, marginally ciliolate, glabrous to puberulent on the back. Ray florets 8 or 9; corollas 7–11.5 mm long, yellow, often becoming whitish with purple veins when dry, glandular-puberulent below. Disc florets 20–50; corollas 3–5 mm long, yellow, bilabiate, with the narrow lobe ca. 4 times as long as the teeth on the broad lobe, glandular puberulent on the tube and throat. Achenes cylindric to narrowly clavate, 2.3–4 mm long; ray achenes glabrous on the surface appressed against the subtending phyllaries, otherwise strigillose to villous; disc achenes evenly pubescent. Pappus of the rays biaristate or coroniform; the disc pappus coroniform or double. Chromosome number (from var. *sonorae* only): $n = 12$.

DISTRIBUTION: Southern Sonora to northern Nayarit. Locally common in thorn forest and semi-desert sites (Figure 10).

Pectis purpurea is apparently most closely related to *P. sinaloensis*. Unlike most species in sect. *Pectothrix*, both of these have glands scattered on the undersurface of the leaves or in submarginal rows on the undersurface. In addition, these species both have many-flowered heads, angular-obovate phyllaries and a biseriate disc pappus (except in one variety of *P. purpurea*). Although some forms of *P. purpurea* resemble *P. rusbyi* (Keil, 1974), the relationship between these two species is not as close as that between *P. purpurea* and *P. sinaloensis*.

8a. **Pectis purpurea** Brandeg., Zoe **5:** 225. 1905. var. **purpurea.** Figure 9.

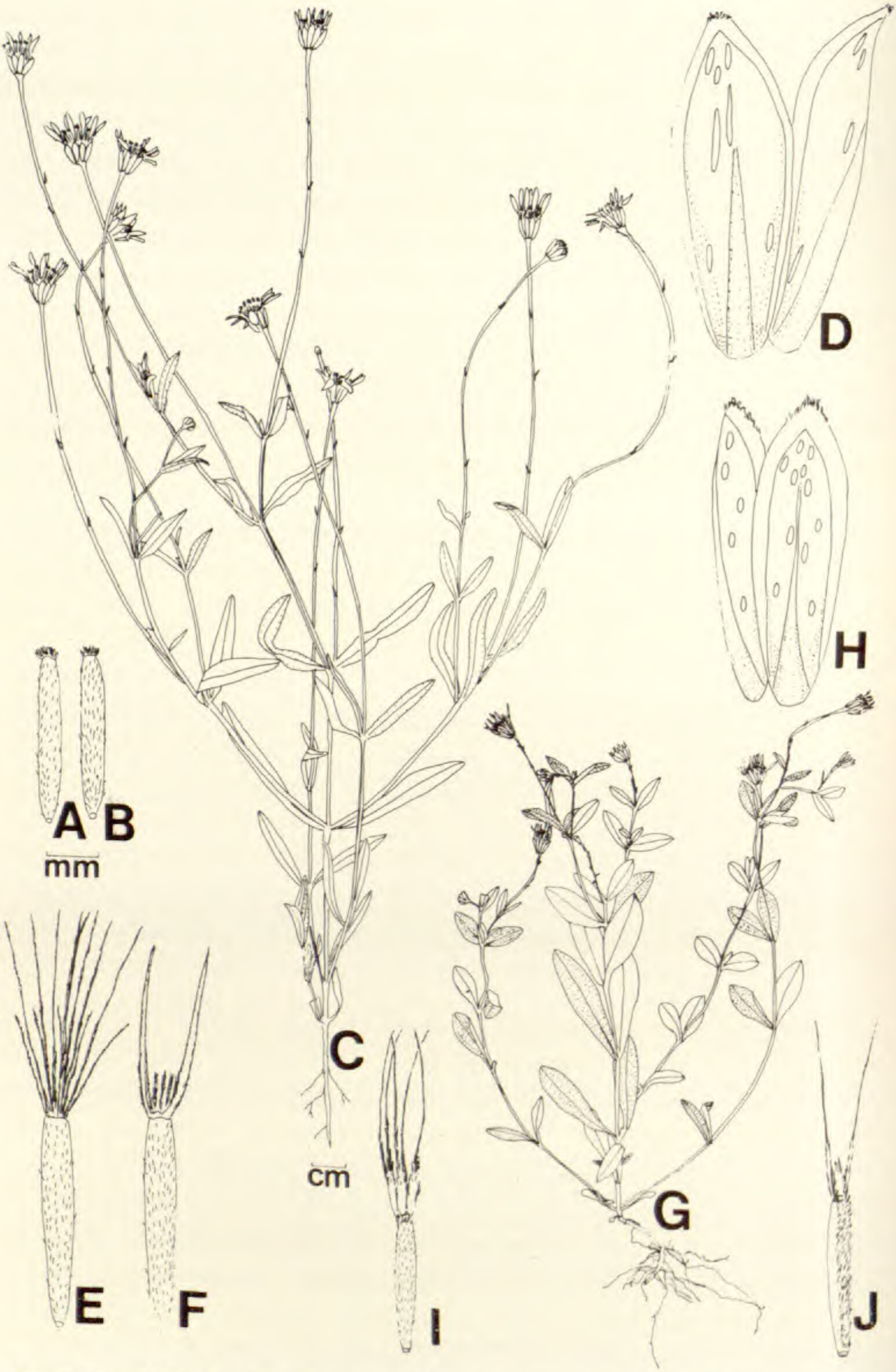


Figure 9. A-F, *Pectis purpurea;* A-B, var. *purpurea* (*Gentry 5044,* MO); C-F, var. *sonorae* (*Keil & Canne 8737,* OS); G-J, *Pectis sinaloensis* (*Keil & Canne 8810,* OS). A, E, I, disc achenes; B, F, J, ray achenes; C, G, habit; D, H, phyllaries.

Stems to 50 cm, minutely puberulent on the angles or glabrate. Leaves 1.5–4.5 cm long, 1–4 mm broad, acute to acuminate, mucronate, ciliate near the base with 1–3 pairs of bristles 1–3 mm long, glabrous, punctate with glands 0.4–0.7 mm in diameter scattered on the undersurface or in submarginal rows. Peduncles 6–11 cm long, glabrous, with 5–7 bracteoles 1–1.5 mm long. Phyllaries 4–4.8 mm long, 1–1.3 mm broad, glabrous, punctate with 5–10 glands in two vertical rows or scattered. Ray corollas 7–8 mm long, 1–1.3 mm broad. Disc corollas 20–40, 3–3.3 mm long. Ray achenes 2.3–3 mm long, strigillose; disc achenes 3.3–3.7 mm long, strigillose. Pappus of both ray and disc coroniform, 0.3 mm long. Chromosome number unknown. Flowering October to February.

DISTRIBUTION: Known only from the vicinity of the type locality in central Sinaloa at ca. 200 m elevation (Figure 10).

Pectis purpurea var. *purpurea* has been collected several times in and around Cofradia, Sinaloa since its initial discovery by T. S. Brandegee. There is no evidence of intergradation of pappus structure between this variety and the other two varieties of *P. purpurea,* such as are found in some other species of sect. *Pectothrix.* The very local and isolated range of var. *purpurea* has apparently allowed this race to maintain its identity.

REPRESENTATIVE SPECIMENS: **Mexico.** SINALOA: Cofradia, *Gentry 5044* (ARIZ. MO); Cofradia, *Gentry 5496* (ARIZ. MO).

8b. **Pectis purpurea** Brandeg. var. **sonorae** Keil, Brittonia **26:** 35. 1974. TYPE: **Mexico.** SONORA: 1.9 mi NW of Vicam on Mexico Rte 15, ca. 66 mi SE of Guaymas, *Canne & Keil 8644* (Holotype, US!; isotypes, ARIZ!, ASU!, DES!, DS!, ENCB!, F!, GH!, MICH!, MO!, NY!, OS!, RSA!, SD!, SMU!, TEX!, UC!).

Figure 9.

Stems to 50 cm, glabrous to densely puberulent. Leaves 1.5–6 cm long, 2.5–9 mm broad, obtuse to acute, mucronate, ciliate near the base with 1–3 pairs of bristles 1–2.4 mm long, glabrous to densely puberulent on the upper surfaces, glabrous or puberulent on the midribs below, punctate with glands 0.4–0.7 mm in diameter in submarginal rows on the undersurface. Peduncles 4–13 cm long, glabrous to densely puberulent, with 4–10 brac-

teoles ca. 2 mm long. Phyllaries 5–6.5 mm long, 1.8–3 mm wide, glabrous or puberulent, punctate with 4–12 scattered glands. Ray corollas 9–11.5 mm long, 2–3 mm wide. Disc florets 40–50, the corollas 4–5 mm long. Ray and disc achenes both 3–4 mm long, pilose or strigillose. Pappus of the rays biaristate, 2–3 mm long, with 1–4 short scales between the awns on the side adjacent to the subtending phyllary; pappus of the disc biseriate, the inner series of 5–10 stiff bristles 4–5 mm long, the outer series of 8–20 shorter, more slender bristles. Chromosome number: $n = 12$. Flowering August and September.

DISTRIBUTION: Southern Sonora and northern Sinaloa along the coastal plain (Figure 10).

Pectis purpurea var. *sonorae* is the most widespread and most variable of the three varieties of *P. purpurea*. The pubescence of the plants of var. *sonorae* ranges from subglabrous to densely puberulent within individual populations. The plants of this variety appear to be somewhat weedy and are often locally abundant. Some of the areas where this variety is found are heavily browsed, but *P. purpurea* does not appear to be touched. Perhaps the strongly scented foliage serves as a deterrent to browsing as the oils have a very disagreeable odor resembling that of stinkbugs (Pentatomidae).

REPRESENTATIVE SPECIMENS: see Keil (1974) for specimen citations for *Pectis purpurea* var. *sonorae*.

8c. **Pectis purpurea** Brandeg. var. **lancifolia** (Greenm.) Keil, Brittonia **26:** 36. 1974. TYPE: **Mexico.** NAYARIT: between Concepción and Acaponeta, *Rose 1893* (Lectotype, GH!; isolectotypes, GH!, US!).

Pectis sinaloensis Fern. var. *lancifolia* Greenm., Proc. Am. Acad. **40:** 50. 1904.
Pectis lancifolia (Greenm.) Rydb., N. Am. Fl. **34:** 203. 1916.

Stems to 40 cm, hirtellous on the angles. Leaves 2–3 cm long, 3–6 mm broad, acute, mucronate, ciliate along the margins with 4–6 pairs of bristles 2–3 mm long, densely short puberulent on the upper surfaces, hirtellous along the midribs beneath, punctate with glands ca. 0.25 mm diameter both submarginal and scattered on the undersurface. Peduncles 7–12 cm long,

short puberulent, with 4–8 bracteoles ca. 3 mm long. Phyllaries 5–5.5 mm long, 1.6–2 mm broad, glabrous or minutely puberulent, punctate with 4–6 scattered glands. Ray corollas 9–10 mm long, 2–3 mm wide. Disc florets ca. 40, the corollas 4.5–4.8 mm long. Ray and disc achenes both ca. 3.5 mm long, strigillose. Pappus of the rays biaristate, 3–4 mm long, with ca. 8 short scales between the awns on the side adjacent to the subtending phyllary; pappus of the disc biseriate, the inner series of 4–6 stiff bristles ca. 6 mm long, the outer series of 8–16 flattened, fimbriate pales to 2 mm long. Chromosome number unknown.

DISTRIBUTION: Known only from the type collection in northern Nayarit (Figure 10).

Pectis purpurea var. *lancifolia* is somewhat of an enigma. Known only from its type collection, this taxon is clearly a member of the *P. purpurea* complex. It is far removed geographically, however, from the nearest population of var. *sonorae,* which it most closely resembles. *Pectis purpurea* var. *lancifolia* may represent a relict population of a once more widespread *P. purpurea,* or conversely, may be a pioneer population. In either case, its present status is rather uncertain, because extensive modification of the habitat has occurred in the region where the type collection was made; in fact, this variety may well be extinct.

9. **Pectis sinaloensis** Fern., Proc. Am. Acad. **33:** 69. 1897. TYPE: **Mexico.** SINALOA: Mazatlán, *Wright 1204* (Lectotype (here chosen), GH!; isolectotypes, F!, MO!, MSC!, US!). Figure 9.

Unscented, tap-rooted annuals, usually branching from the base. Stems 10–30 cm long, erect, or more commonly decumbent, branching above, short villous in lines or glabrate. Leaves linear-lanceolate, elliptic or oblanceolate, 1–5 cm long, 5–12 mm wide, obtuse to acutish, mucronate, basally ciliate with 2–6 pairs of bristles 1–3 mm long, glabrous or puberulent at the base, punctate on the undersurface with numerous scattered round oil glands. Peduncles 2–6 cm long, glabrous, with 4–6 scale-like bracteoles 1–2 mm long. Heads terminal and axillary, few. Phyllaries 8 (rarely 9 or 10), oblanceolate, 5 mm long, 1.5 mm wide, rounded

to subacute, broadly hyaline-margined, dorsally rounded, basally gibbous, apically short-ciliolate, otherwise glabrous, punctate with 6-12 scattered elliptical oil glands. Ray florets 8–10; corollas 5–7 mm long, with narrowly to broadly ovate glabrous ligules and sparsely glandular-puberulent tubes. Disc flowers 25–60; corollas 4–5 mm long, bilabiate, with the narrow lobe ca. 2 mm long, two or three times the length of the teeth on the broad lobe, sparsely glandular-puberulent. Achenes 2–3 mm long, those of the disc sparsely strigillose all over, those of the rays glabrous on the side adjacent to the subtending phyllary, otherwise densely strigillose. Pappus of the rays biaristate, 2–3 mm long, with a single fimbriate scale between the bristles on the side adjacent to the subtending phyllary. Pappus of the disc biseriate, of 5 stiff, antrorsely scabrid bristles 3–3.5 mm long, alternating with 5 fimbriate acute to bristle-tipped scales 1–2 mm long. Chromosome number: $n = 12$. Flowering September to January.

DISTRIBUTION: Known only from the coast of Sinaloa at a few meters elevation (Figure 10). This species is particularly common on the sea-cliffs at Mazatlán, the type locality.

At Altata, Sinaloa, *Pectis sinaloensis* has formed an extensive hybrid swarm with *Pectis papposa* var. *papposa*. T. S. Brandegee described *Pectis salina* from this population. The types of *P. salina* are intermediate between *P. sinaloensis* and *P. papposa*. The hybrids in this population are apparently fertile, and no detectable chromosomal irregularities were detected in any of the members of the population that I examined cytologically. Plants with varying degrees of intermediate characters are found in the population with extreme forms approaching both parents. Because of its origin, therefore, this hybrid population is to be known as *Pectis* × *salina* Brandegee, pro sp.

The plants in the *Pectis sinaloensis* population at Altata possess somewhat larger heads than those at Mazatlán. This feature may well be a result of instability introduced into the *P. sinaloensis* population by the long-term hybridization with *P. papposa*. If this is the case, there may not be any "pure" *P. sinaloensis* at Altata, only extremes of the hybrid swarm.

REPRESENTATIVE SPECIMENS: **México.** SINALOA: Mazatlán, *K & C 8810* (OS); La Neveria, N of Mazatlán, *Mexia 1094* (CAS, F, GH, MICH, MO, NY, US).

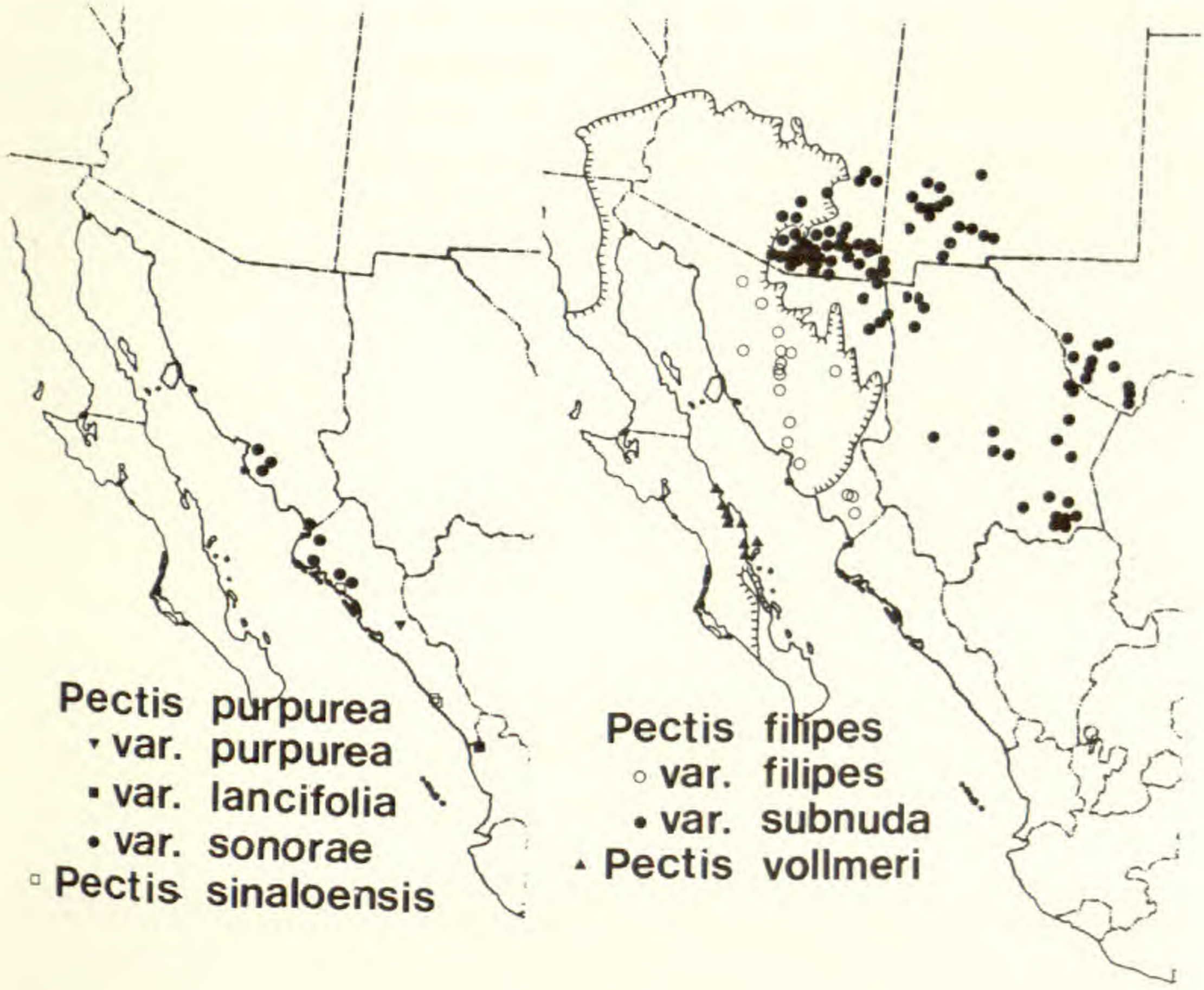


Figure 10. Geographical distribution of *Pectis purpurea, P. sinaloensis, P. filipes* and *P. vollmeri.* Half-barred line indicates Sonoran Desert boundary (redrawn from Shreve, 1942).

10. **Pectis filipes** Harv. & Gray in A. Gray, Mem. Am. Acad. **4:** 62. 1849. TYPE: **Mexico.** "CALIFORNIA," (probably collected in Sonora near Guaymas or Hermosillo), *Coulter 329* (Holotype, TCD!; isotypes, GH (fragment)!, K!). Figure 11.

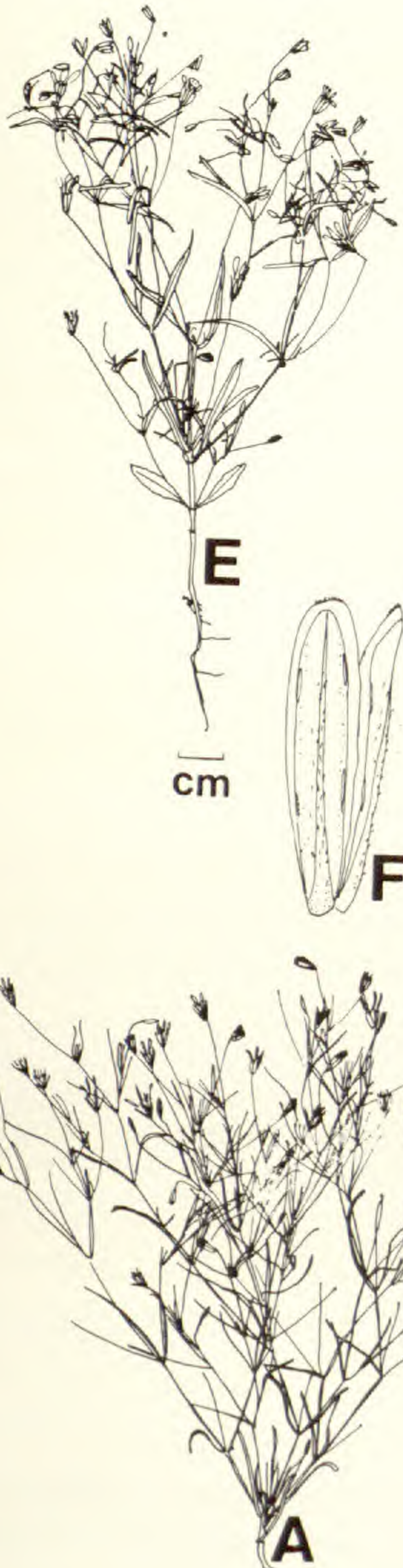
Strong-scented, diffusely branched tap-rooted annuals. Stems 5–40 cm long, slender, pseudodichotomously branched, glabrous or puberulent. Leaves linear to narrowly elliptic, 1–6 cm long, 0.5–5.5 mm wide, often strongly revolute, basally ciliate with 1–4 pairs of bristles 1–2 mm long, otherwise entire, glabrous or puberulent, marginally punctate with rounded oil glands ca. 0.5 mm diameter. Peduncles filiform, 1–6.5 cm long, glabrous or puberulent, with 1–3, usually subterminal, lanceolate bracteoles ca. 1 mm long. Heads solitary in the forks of the stem, cylindric to narrowly campanulate. Phyllaries 5, narrowly oblong

to oblong-obovate 3.5–6 mm high, ca. 1 mm broad, basally truncate and gibbous, apically ciliolate, obtuse to acute, hyaline margined, convex and slender-keeled, glabrous or puberulent, punctate with 0–2 small to large subterminal glands and 2–3 pairs of smaller, rounded to elongated submarginal glands. Ray florets 5; corollas 4–9 mm long, with narrowly to broadly obovate glabrous ligules and glandular-puberulent tubes. Disc florets 2–22; corollas 2.5–4 mm long, bilabiate, with the narrow lobe ca. twice the length of the teeth on the broad lobe, sparsely to densely glandular-puberulent. Achenes 2.5–4 mm long, shorter than the phyllaries, strigillose or short pilose with bifurcate hairs. Pappus 0–3 aristate, antrorsely barbed to nearly smooth, usually with an additional low crown ca. 0.2 mm high. Chromosome number: $n = 12$.

DISTRIBUTION: Southeastern Arizona and western Texas to southern Sonora and southern Chihuahua at elevations of 0–2000 meters (Figure 10). Within the broad altitudinal tolerances of *Pectis filipes,* two varieties may be distinguished. The typical variety has a primarily Sonoran Desert distribution, occurring mostly below 500 meters elevation. The variety *subnuda* grows mostly at higher elevations and barely reaches the fringes of the Sonoran Desert. This latter variety occurs mostly in the grassland and pine-oak-juniper zones and extends eastward into the Chihuahuan Desert.

Both varieties of *Pectis filipes* occasionally grow together with other species of sect. *Pectothrix* and sometimes form hybrids with these species. The variety *subnuda* locally hybridizes with *P. pringlei* in Chihuahua, with *P. papposa* var. *grandis* in New Mexico, and with *P. papposa* var. *papposa* in Arizona. The variety *filipes* hybridizes with both *P. papposa* var. *papposa* and with *P. rusbyi.* In one locality south of Hermosillo, Sonora, all three of these taxa were found to be involved in a single complex hybrid swarm.

Although interspecific hybridization involving *Pectis filipes* is relatively common, there is little evidence to suggest that the effects of the crossing are more than local. Throughout most of its range, *P. filipes* remains well differentiated from other species in the section. At the local populational level, some bizarre recombination types have been observed which combine the features of two or more species.



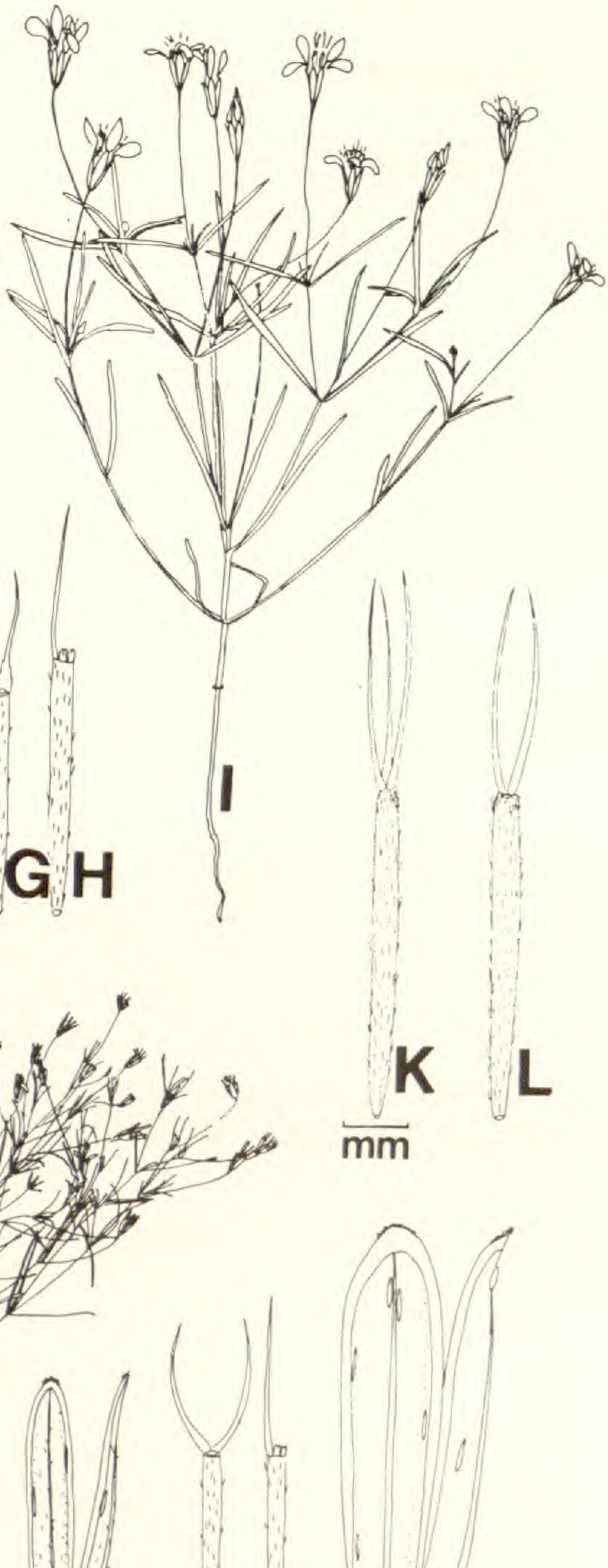


Figure 11. A-H, *Pectis filipes;* A-D, var. *filipes* (*Keil & Canne 8659,* OS); E-H, var. *subnuda* (*Keil & McGill, 8512,* OS); I-L, *Pectis vollmeri* (*Carter & Moran 5250,* CAS). A, E, I, habit; B, F, J, phyllaries; C, G, K, disc achenes; D, H, L, ray achenes.

10a. **Pectis filipes** Harv. & Gray in A. Gray, Mem. Am. Acad. **4:** 62. 1849. var. **filipes.** Figure 11.

Herbage densely puberulent. Leaves linear, 1–3 cm long, 0.5–2.5 mm wide. Fascicles of several short narrow leaves usually developed in upper axils. Peduncles 1–2.5 (–3.5) cm long. Involucre cylindric; phyllaries acute, lacking subterminal oil glands. Disc florets 2–8; corollas 2.5–3.5 mm long. Oils of plants from southern Sonora lemon-scented, from other populations spicy-scented. Chromosome number: $n = 12$. Flowering August to October.

DISTRIBUTION: Central and southern Sonora, mostly below 500 meters elevation (Figure 10).

Coulter's type locality was listed as "California," a state where *Pectis filipes* is not known to occur. Rydberg (1916) suggested that this species was collected by Coulter in Arizona. Coulter's itinerary in Arizona (Coville, 1895), however, did not include any areas where *P. filipes* grows. Upon examination of the type of *P. filipes,* I found that it very closely resembles the Sonoran race of the species. Coulter is known to have collected at both Guaymas and Hermosillo, Sonora (Coville, 1895; McVaugh, 1943), and therefore it is likely that the type collection of *P. filipes* came from this region.

REPRESENTATIVE SPECIMENS: **México.** SONORA: 28 mi S of Hermosillo, *K & C 8617* (OS); 11.8 mi E of jctn. w/Mexico 15 on rd. to Álamos, *K & C 8665* (OS); 14 mi S of Divisaderos, *Wiggins 7469* (ARIZ, DS, MO, TEX, US).

10b. **Pectis filipes** Harv. & Gray in A. Gray var. **subnuda** Fern., Proc. Am. Acad. **33:** 76. 1897. TYPE: **Mexico.** CHIHUAHUA: Janos, *A. Schott s.n.* (Lectotype (here chosen), GH!). Figure 11.

Herbage glabrous to moderately puberulent. Leaves linear to narrowly elliptic, 1–6 cm long, 1–5.5 mm wide. Peduncles (1–) 2–6.5 cm long. Involucres cylindric to campanulate; phyllaries obtuse to acute, with or without subterminal oil glands. Disc florets 7–22; corollas 3–4 mm long. Oils spicy-scented but not lemon-scented. Chromosome number: $n = 12$. Flowering July to November.

DISTRIBUTION: Southeastern Arizona and western Texas to northeastern Sonora and southern Chihuahua, mostly at 1000–3000 meters elevation (Figure 10).

The present treatment of *Pectis filipes* var. *subnuda* as a widespread eco-geographical race differs markedly from the much more restricted concept of Fernald (1897), who considered var. *subnuda* to be merely a minor morphological variant in the much more widespread species, *P. filipes.* As the epithet, *subnuda,* is available in the varietal rank and my concept of the upper elevation race of *P. filipes* includes the types of var. *subnuda* I have necessarily used this epithet for the redefined variety.

REPRESENTATIVE SPECIMENS: **México.** CHIHUAHUA: 10–14 mi W of Hidalgo del Parral, *Gentry 8257* (GH, MICH, US); 5.4 mi N of Janos, *K & M 8414* (OS); Mts. NW of Chihuahua, *LeSueur 1019* (CAS, F, GH, MO, TEX, UC). SONORA: Guadelupe Canyon, *Mearns & Merton 2048* (DS, NY, US); N of Horconcitos, *Phillips 848* (ARIZ, MICH).

United States. ARIZONA: Cochise Co.: Chiricahua Mts., *Blumer 1708* (ARIZ, DS, F, GH, KSC, MO, NMC, NY, US); Bowie, *Jones 4227* (ARIZ, DS, F, MICH, MO, NMC, NY, PH, POM, UC, US); Greenlee Co.: Big Lue Range, *Gould & Haskell 4091* (ARIZ, CAS, DS, F, NY, UC); Pima Co.; Santa Rita Mts., *Pringle s.n.* (CAS, F, GH, MICH, MO, NY, PH, US). NEW MEXICO: Grant Co.: 18 mi NW of Silver City, *Metcalfe 685* (ARIZ, MO, ND-G, NMC, NY, POM, UC); Burro Mts., *Rusby 185* (F, MICH, MO, NY, PH, UC, US); Coppermine Creek, *Wright 1125* (GH, K, MO, NY, PH, TCD, UC, US); Sierra Co.: Black Range, *Metcalfe 1357* (CAS, F, GH, MO, NMC, NY, POM, UC). TEXAS: Brewster Co.: Big Bend Nat'l. Park, *Correll & Correll 35379* (ENCB, MICH, SD, TEX, US); 15.1 mi N of Castolon, *K & M 7797* (OS).

11. **Pectis vollmeri** Wiggins, Contr. Dudley Herb. **4:** 27. 1950.
TYPE: **Mexico.** BAJA CALIFORNIA SUR: foot of Coyote Grade 20 mi S of Mulegé, *Wiggins 11407* (Holotype, DS!; isotypes, CAS!, DS!, GH!, UC!, US!). Figure 11.

Strong-scented, tap-rooted annuals. Stems 5–50 cm long, erect to decumbent, pseudodichotomously branched, glabrous, purplish. Leaves linear, 1–6 cm long, 1–2 mm broad, often revolute, basally ciliate with 2–3 pairs of bristles 1–2 mm long, rarely with 1–3 short basal lobes, otherwise entire, glabrous, marginally punctate with round to elliptic oil glands ca. 0.3 mm diameter. Peduncles 3–8 cm long, glabrous, with 2–3 scattered, linear acuminate glabrous bracteoles 1–2 mm long. Heads solitary in the forks of the stem. Phyllaries 5, narrowly obovate, 6–8 mm long, 1.5–2.5 mm broad, apically obtuse, ciliolate, basally truncate and

gibbous, hyaline-margined, convex on the back, round-keeled below, glabrous, punctate with 0–3 small, rounded subterminal oil glands, and 3–7 pairs of narrow scattered submarginal glands. Ray florets 5; corollas 6–10 mm long, with broadly ovate glabrous ligules and glandular-puberulent tubes. Disc florets 9–19; corollas 4–5 mm long, weakly bilabiate with the narrow lobe ca. twice as long as the teeth on the broad lobe, glandular-puberulent on the tube and throat. Achenes 4–6 mm long, cylindric, strigillose to short pilose. Pappus 2–6 aristate; awns stiff, spreading, 3–4 mm long, purplish, antrorsely scabrid toward the tips. Chromosome number unknown. Flowering September to November and again from February to April.

DISTRIBUTION: Endemic to a narrow strip along the eastern coast of Baja California at elevations of 0-500 meters (Figure 10).

Pectis vollmeri appears to be most closely related to *P. filipes.* Both species share the characteristics of slender, diffuse habit, five-rayed heads, and aristate pappus. *Pectis vollmeri,* however, is somewhat stouter and has larger heads and flowers. Wiggins (1950) suggested that *P. vollmeri* was closely related to *P. linifolia* L. of sect. *Pectidium.* Although both species do have similar pappus structure, the two taxa differ greatly in size of the florets, number of disc florets, placement and size of foliar oil glands, glandularization of the disc corollas and in overall habit. In my opinion, the relationship between *P. vollmeri* and *P. linifolia* is distant, and the similarities in pappus structure are the result of parallel evolution rather than of patristic relationship.

REPRESENTATIVE SPECIMENS: **México.** BAJA CALIFORNIA SUR: 40.6 mi S of Mulegé, *Carter, Alexander & Kellogg 1988* (DS, GH, US); SW of Santa Rosalia, *Carter & Kellogg 3082* (CAS, GH, MO, SD, US); Rancho Aguajito, *Carter & Moran 5250* (CAS, SD, UC, US); Coyote Bay, *Gentry 4068* (ARIZ, DS, GH, MO, UC, US); Arroyo de San José de Magdalena, *Wiggins 11386* (DS, GH, UC, US).

DOUBTFUL AND EXCLUDED TAXA

Pectis aquatica S. Wats., Proc. Am. Acad. **23:** 279. 1888. TYPE: **Mexico.** CHIHUAHUA: at base of Sierra Madre (S of Cd. Guerrero), *Pringle 1296* (Holotype, GH!; isotypes, F!, MO!). =**Hydropectis aquatica** (S. Wats.) Rydb.

Pectis fasciculata Poir. in Lam. & Poir., Encycl. Method. Bot. **5:** 120. 1804. TYPE: grown from seed of unknown origin (no type specimens located). This species is indeterminable.

Pectis multiradiata Sesse & Mocino, Fl. Mex. ed. 2. 190. 1894. TYPE: **Mexico.** SINALOA: prope Oppidum (no type specimens located). This species is indeterminable.

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DEPARTMENT OF BOTANY
THE OHIO STATE UNIVERSITY
1735 NEIL AVENUE
COLUMBUS, OHIO 43210

Present address:
BIOLOGICAL SCIENCES DEPARTMENT
CALIFORNIA POLYTECHNIC STATE UNIVERSITY
SAN LUIS OBISPO, CALIFORNIA 93407

CHROMOSOME STUDIES IN NORTH AND CENTRAL AMERICAN SPECIES OF PECTIS L. (COMPOSITAE: TAGETEAE)

DAVID J. KEIL

Chromosomal modification is often a major factor in the evolutionary diversification of a large, rapidly evolving genus. *Pectis,* the largest and most widespread genus in the New World tribe Tageteae (Compositae), has radiated into a variety of habitats during its evolutionary history. Until relatively recently, however, little has been known of the role of chromosomal change in the evolution of the genus. *Pectis* was cytologically unknown until the studies of Raven and Kyhos (1961) and of Turner, Ellison, and King (1961). Subsequently, additional counts have been reported for several taxa (Table 1). To date, however, only a few of the species have been studied cytologically, and these only from a few populations. Of the four large genera of the Tageteae, *Pectis* has been the most poorly represented in cytological studies.

This investigation is one of a series of studies of the evolution and taxonomy of *Pectis.* The genus reaches its greatest diversity in the warmer areas of North America, and it is from this region that most of the collections upon which this study is based were made. Through an examination of the chromosomes of as many species as possible, and from numerous populations of wide-ranging species, information regarding the variability of chromosomes in *Pectis* can be better correlated with the evolutionary history and systematics of the genus.

MATERIALS AND METHODS

Immature capitula were killed and fixed in the field in modified Carnoy's fixative (4 chloroform : 3 ethanol : 1 glacial acetic acid), and were kept under refrigeration prior to examination. In a modification of the methods of Beeks (1955), whole floret buds were stained (usually without heat) for 2–48 hours in standard 1% acetocarmine or iron acetocarmine solution and were squashed without prior maceration in a drop of Hoyer's solution. Camera lucida drawings were prepared from meiotic microsporocytes to document each reported count.

Table 1. **Previously reported chromosome counts for Pectis.**

Reported count (*n*)	Taxon	Reference
	P. angustifolia Torr. var. *angustifolia*	
12	*(as P.* cf. *texana* Cory)	Powell & Turner (1963)
12	(as *P. angustifolia* Torr.)	Powell & Turner (1963)
	P. angustifolia Torr. var. *tenella* (DC.) Keil	
12	(as *P. tenella* DC.)	Powell & Turner (1963); Strother (1972); Urbatch in Löve (1974)
12	*P. coulteri* Harv. & Gray	Keil (1975B)
12	*P. depressa* Fern.	Powell & Turner (1963)
	P. filipes Harv. & Gray var. *subnuda* Fern	
12	(as *P. filipes* Harv. & Gray)	Powell & Sikes (1970); Fay in Löve (1974)
ca. 24	*P. latisquama* Sch. Bip. ex Greenm.	Powell & Turner (1963)
12	*P. multiseta* Benth. var. *ambigua* (Fern.) Keil	Keil (1975B)
12	*P. multiseta* Benth. var. *multiseta*	Keil (1975B)
	P. papposa Harv. & Gray var. *papposa*	
12	(as *P. papposa* Harv. & Gray)	Raven & Kyhos (1961); Watson (1973)
12	*P. papposa* Harv. & Gray var. *grandis* Keil	Keil (1974); Keil & Stuessy (1975)
12, 12 + fragment	(as *P. papposa* Harv. & Gray)	Powell & Sikes (1970)
12	*P. pringlei* Fern.	Fay in Löve (1974)
12	*P. purpurea* Brandeg. var. *sonorae* Keil	Keil (1974)
12	(as *P. palmeri* S. Wats.)	Turner & Flyr (1966)
	P. rusbyi Greene ex A. Gray	
12	(as *P. palmeri* S. Wats.)	Turner & Flyr (1966)
12	(as *P. puberula* Greenm.)	Turner & Flyr (1966)
12	*P. saturejaoides* (Mill.) Sch. Bip.	Turner, Ellison & King (1961); Powell & Turner (1963)
12	*P. sinaloensis* Fern.	Turner & Flyr (1966)
36	*P. subsquarrosa* (Hook. f.) Sch. Bip.	Kyhos in Wiggins & Porter (1971)

RESULTS AND DISCUSSION

Chromosome counts were obtained from 28 taxa and from five natural interspecific hybrids (Table 2; Figures 1–34). Of the taxa studied, 22 are diploids with $n = 12$, three are tetraploids with $n = 24$, one has both a diploid and a tetraploid race, and two are hexaploids with $n = 36$. Two of the hybrids are triploids with 8–12 bivalents and correspondingly 12–20 univalents at metaphase I and with very irregular meiotic behavior. The remaining hybrids are functional diploids with only sporadic incidence of meiotic irregularities. Supernumerary chromosomes were noted in three species and in some of the interspecific hybrids. Of the counts reported, 18 of the taxa and all of the interspecific hybrids are first reports.

Several evolutionary lines are represented in the newly reported counts. Some of these lines correspond to named sections of the genus. However, since sectional limits have never been applied to the entire genus, and in some cases, previously published sectional limits have been found to be in error (Keil, 1977), not all taxa are presently assignable to sections. Consequently, in the following discussion, taxa will be referred to section only when the affinities are well established.

Section *Pectothrix* A. Gray is easily the best-known portion of the genus cytologically. Counts are known for all except two species, *Pectis vollmeri* Wiggins and the newly described *P. peruviana* Keil (Keil, 1977), although varieties remain uncounted in two other species. First reports for this section are two western Mexican taxa, *P. filipes* var. *filipes* and *P. stenophylla* var. *biaristata,* a Chihuahuan Desert endemic, *P. incisifolia,* and a Texas endemic, *P. angustifolia* var. *fastigiata.* Numerous additional counts are reported for *P. angustifolia* vars. *angustifolia* and *tenella, P. filipes* var. *subnuda, P. papposa* vars. *papposa* and *grandis, P. pringlei, P. rusbyi,* and *P. sinaloensis.*

Section *Pectothrix* is interesting from the standpoint of chromosomal uniformity and the relative lack of sterility which characterize the known natural hybrids within the group. Of the various hybrid combinations which have been studied cytologically, only one, *Pectis angustifolia* var. *angustifolia* × *P. papposa* var. *grandis,* was found to possess individuals displaying meiotic irregularities. Inversion bridge-fragment formations and

Table 2. **New chromosome counts for taxa of Pectis.**

Chromosome number (*n*)	Taxon with location and voucher[a]
12	**Pectis angustifolia** Torr. var. **angustifolia** **México.** CHIHUAHUA: 13.6 mi S of Cd. Jiménez, *K & M 8387A;* 25.6 mi N of Janos, *K & M 8432A, B.* DURANGO: 1.8 mi E of Nazareno, *K & M 8014A.* **United States.** COLORADO: Fremont Co.: Indian Spring Campground, *K 7637A;* Canyon City, *K 7638* (Figure 1); Sedgwick Co.: 1.5 mi S of Ovid, *K 7634.* NEBRASKA: Keith Co.: 1 mi S of Ogallala at S Platte River, *Stuessy & Stuessy 1717;* Keith-Lincoln Co. line at S Platte River, *K 7635;* Lincoln Co.: S Platte River at Hershey Rd, *K 7603;* S Platte River at Sutherland, *K 7620A.* NEW MEXICO: Grant Co.: S of Sherman along Mimbres River, *K & M 8465A;* 6.5 mi E of Santa Rita, *K & M 8740;* 4 mi N of Silver City, *K & M 8481A*[b]; Hidalgo Co.: 7.2 mi NE of jctn. w/US 70 on NM 90, *K & M 8494A.* TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7795A;* 15.1 mi N of Castolon, *K & M 7798A;* Culberson Co.: 1.4 mi SE of Hudspeth Co. line on I-10, *K & M 7687;* Hudspeth Co.: SE of Ft Hancock, *K & M 7665A, B;* Presidio Co.: 18.5 mi S of Marfa, *K & M 7741;* 13.1 mi SE of Presidio, *K & M 7774A, B.*
12*	**Pectis angustifolia** Torr. var. **fastigiata** (A. Gray) Keil **United States.** TEXAS: Sutton Co.: Sonora, *Keil & Roberts 10074* pop. (Figure 2).
12	**Pectis angustifolia** Torr. var. **tenella** (DC.) Keil **México.** COAHUILA: 107 mi S of Piedras Negras, *K & M 7849A, B, C;* 114 mi S of Piedras Negras, *K & M 7860A;* between Nueva Rosita and Monclova, *K & M 7865A;* 11.4 mi S of Monclova, *K & M 7875;* 27 mi S of Monclova, *K & M 7879A, B* (Figure 3); 60 mi S of Monclova, *K & M 7911A;* 22.5 mi E of Paila, *K & M 7944A;* 16.7 mi E of Paila, *K & M 7950A, B;* 5.3 mi E of Paila, *K & M 7954A*[c]; 13 mi W of Paila, *K & M 7960A, B;* 8.6 mi E of Emiliano Zapata, *K & M 7996;* 4.2 mi S of Acatita, *K & M 8052A;* 2.1 mi N of Acatita, *K & M 8065A;* 7.8 mi N of Acatita, *K & M 8072A;* 1.1 mi S of Rancho El Cinco, *K & M 8102A;* 10.3 mi S of Rancho los Charcos, *K & M 8165A, B.* DURANGO: E of Mapimí, *K & M 8186A.* **United States.** TEXAS: Hidalgo Co.: 0.8 mi E of jctn. w/Texas FM rd 886 on US 83, *K & C 9247A, B;* Starr Co.: 1 mi W of jctn. w/Texas FM rd 1430 on US 83, *K & C 9248B;* 11.6 mi SE of jctn. w/Texas FM rd 2098 on US 83, *K & C 9249A.*

Table 2 — continued

Chromosome number (*n*)	Taxon with location and voucher
12*	**Pectis berlandieri** DC. **México.** TAMAULIPAS: just E of Magiscatzan, *K & C 9235 A, B, C;* 3 mi E of Mante, *K & C 9238B;* 8.9 mi W of Magiscatzan, *K & C 9240A* (Figure 4), *B.*
24*	**Pectis bonplandiana** H.B.K. **Guatemala.** SUCHITEPEQUEZ: Puente Siguacan, *K 9439A* (Figure 5); 5.4 km E of jctn. w/rd to Chicanoa on CA–2, *K 9442A;* 11.5 km E of Puente Siguacan on CA–2, *K9448A*[d].
12*	**Pectis capillipes** (Benth.) Hemsl. **Honduras.** CHOLUTECA: just S of San Antonio de Flores, *K 9505A* (Figure 6), *B,* pop.; 8.4 km W of Choluteca *K 9517* pop.
24*	**Pectis cylindrica** (Fern.) Rydb. **México.** COAHUILA: 9.4 mi S of Rancho los Charcos, *K & M 8161* pop. (Figure 7). SONORA: 28.5 mi W of Álamos, *K & C 8663* pop.
12*	**Pectis filipes** Harv. & Gray var. **filipes** **México.** SONORA: 28 mi S of Hermosillo, *K & C 8617A, B, C;* 3.8 mi E of jctn. w/Mexico 15 on rd to Álamos, *K & C 8659A, B;* 11.8 mi E of jctn. w/Mexico 15 on rd to Álamos, *K & C 8665A, B*[e], *C;* 7.2 mi SE of Navojoa, *K & C 8725A* (Figure 8).
12	**Pectis filipes** Harv. & Gray var. **subnuda** Fern. **México.** CHIHUAHUA: 24 mi N of Nueva Casas Grandes, *K & M 8406A, B.* **United States.** ARIZONA: Cochise Co.: 0.5 mi S of Paradise, *K & M 8512A;* Chiricahua Natl Monument, *K & M 8528A* (Figure 9). TEXAS: Presidio Co.: 18.5 mi S of Marfa, *K & M 7742A, B;* 1.4 mi N of Cibola Creek on US 67, *K & M 7749A;* Brewster Co.: 15.1 mi N of Castolón, *K & M 7797A, B, C, D;* 12.5 mi N of Castolón, *K & M 7811A.*

Table 2 — continued

Chromosome number (*n*)	Taxon with location and voucher
12*	**Pectis haenkeana** (DC.) Sch. Bip. **México.** GUERRERO: 3.2 mi S of Iguala, *K & C 9144A, B;* 1.4 mi N of Sabina Grande, *K & C 9115A* (Figure 10), *B;* 22 mi S of Iguala, *K & C 9117A;* 22 mi N of Zumpango del Río, *K & C 9119A, B;* 4.5 mi N of Iguala on México 95–D, *K & C 9137A, B.* MORELOS: 25.7 mi N of Morelos-Guerrero boundary on México 95–D, *K & C 9140A.*
12*	**Pectis incisifolia** I. M. Johnston **México.** COAHUILA: S of Laguna del Rey, *K & M 8101A* (Figure 11), *B, D, E; 8102A; 8105A, B; 8109A, B, C.*
12*	**Pectis leavenworthii** Standl. **México.** MICHOACÁN: 5 mi E of Apatzingan, *Stuessy & Roberts 3744* pop. (Figure 12).
12*	**Pectis longipes** A. Gray **United States.** ARIZONA: Santa Cruz Co.: 2.5 mi N of Sonoita, *K & M 8566A* (Figure 13).
36*	**Pectis multiflosculosa** (DC.) Sch. Bip. **México.** SINALOA: Mazatlán, *Keil & Roberts 10160B;* Mazatlán, *Stuessy & Gardner 3040* pop. (Figure 14).
12*	**Pectis oerstediana** Rydb. **Guatemala.** JUTIAPA: 7.7 km E of jctn. w/rd to Quesada on CA–1, *K 9413B* (Figure 15).
12	**Pectis papposa** Harv. & Gray var. **papposa** **México.** SINALOA: Altata, *K & C 8785A, B, C.* SONORA: 72 mi S of Benjamin Hill on Mexico 15, *K & C 8609A, B;* 12 mi S of Hermosillo, *K & C 8616A, B;* 7 mi NW of Cd. Obregon, *Stuessy & Gardner 3015A, B, C.* **United States.** ARIZONA: Maricopa Co.: 12 mi N of Riggs Rd on I–10, *K & C 8576B;* Pima Co.: 13.6 mi NW of Cortaro Rd exit on I–10, *K & C 8579A;* Pinal Co.: 2.3 mi NW of jctn. w/Storey Rd on I–10, *K & C 8578A.* NEW MEXICO: Hidalgo Co.: 2.5 mi S of I–10 on US 80, *K & M 8496A, B* (Figure 16); Cienega Lake turnoff on US 80, *K & M 8500A.*

Table 2 — continued

Chromosome number (*n*)	Taxon with location and voucher
12	**Pectis papposa** Harv. & Gray var. **grandis** Keil **México.** CHIHUAHUA: 15.4 mi N of Cd Camargo, *K & M 8252–1A;* 20.2 mi N of Janos, *K & M 8429;* 25.6 mi N of Janos, *K & M 8433A.* **United States.** NEW MEXICO: Doña Ana Co.: 28 mi N of Las Cruces, *K 7654A, C* (Figure 17); 1 mi N of jctn, I–10 & I–25, *K 7655A, B.* TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7818A*[1]; El Paso Co.: Horizon City exit on I–10, *K & M 7659A, B;* 2.6 mi NW of Tornillo exit on I–10, *K & M 7664A;* Presidio Co.: 2.7 mi SE of Redford, *K & M 7778A.*
12	**Pectis pringlei** Fern. **México.** CHIHUAHUA: 0.6 mi N of jctn. w/rd to Escalón on México 49, *K & M 8206–2A, B, C;* 29.9 mi S of Jiménez, *K & M 8218A* (Figure 18). COAHUILA: 36.9 mi W of Paila, *K & M 7976A, B, C, D;* jctn. w/rd to San Pedro on México 40, *K & M 7988A, B;* 10.3 mi S of Rancho los Charcos, *K & M 8164A.* DURANGO: 17.5 mi S of Nazareno, *K & M 8033B, C;* 22 mi S of Nazareno, *K & M 8041A.*
12*	**Pectis prostrata** Cav. **El Salvador.** LA LIBERTAD: 1 km E of Santa Tecla, *K9400* pop. **Guatemala.** EL PROGRESSO: 43 km W of El Progresso, *K 9417A;* 23 km W of El Progresso, *K 9418A* (Figure 19). GUATEMALA: 30 km SE of Cd. Guatemala, *K 9398A.* JUTIAPA: 7.3 km W of jctn. w/dirt rd to Jalpatagua on CA–1, *K 9409A.* SANTA ROSA: 3.5 km NW of jctn. w/rd to Culiapa on CA–1, *K 9400A;* 11 km E of Puente Culiapa on CA–1, *K 9405A;* 2.1 km E of jctn. w/rd to Jalpatagua on CA–1, *K 9406A.* ZACAPA: 3.1 km E of Puente Palmilla on CA–1, *K 9424A.* **México.** CHIHUAHUA: 4.5 mi N of Galeana, *K & M 8388.* COAHUILA: 47 mi S of Monclova, *K & M 7901A, C.* MEXICO: 20 mi SSE of Zitacuaro, *Stuessy & Gardner 3126A.* NAYARIT: 44 mi SE of Acaponeta, *K & C 8959A,* pop. SINALOA: 8.7 mi SE of Rosario, *K & C 8948A.* VERACRUZ: 1 mi SE of Tantoyuca, *K & C 9227B.* **United States.** NEW MEXICO: Grant Co.: 6½ mi E of Santa Rita, *K & M 8472* pop.
24*	**Pectis repens** Brandeg. **México.** JALISCO: 6.1 mi E of Nayarit-Jalisco boundary on Mexico 15, *K & C 8993* pop. (Figure 20).
12*	**México.** MÉXICO: 0.5 mi N of Guerrero-México boundary on Federal Rte 55, *K & C 9097* pop. (Figure 21).

Table 2 — continued

Chromosome number (*n*)	Taxon with location and voucher
12	**Pectis rusbyi** Greene ex A. Gray **México.** SINALOA: 20.6 mi S of Sonora-Sinaloa boundary on México 15, *K & C 8738A, B;* 1.8 mi E of San Blas, *K & C 8744A, B, C.* SONORA: just S of Magdalena, *K & C 8594A, B, C*[b], *D;* 7 mi S of Magdalena, *K & C 8595A;* 17 mi S of Hermosillo, *K & C 8614B;* 28 mi S of Hermosillo, *K & C 8621A;* 6.5 mi S of jctn. w/rd to Bahia Kino on Mexico 15, *K & C 8629A;* jctn. w/rd to Bahia San Carlos on Mexico 15, *K & C 8632A;* 0.7 mi S of jctn. w/Sonora 19 on Mexico 15, *K & C 8654* (Figure 22); 14.1 mi W of Álamos, *Stuessy & Gardner 3022* pop.; 29.3 mi W of Álamos, *Stuessy & Gardner 3024* pop. **United States.** ARIZONA: Maricopa Co.: White Tank Mountains, *K 8570* pop.; Yavapai Co.: 2.5 mi S of Beaver Creek Ranger Station, *K 8575AA, BB.*
12	**Pectis saturejaoides** (Mill.) Sch. Bip. **Guatemala.** EL PROGRESSO: 5.6 km E of turnoff to El Rancho on CA–9, *K 9423A* (Figure 23), *B, C;* 0.5 km W of turnoff to El Rancho on CA–9, *K 9427A, B.*
12	**Pectis sinaloensis** Fern. **México.** SINALOA: Altata, *K & C 8786G;* Mazatlán, *K & C 8810A, B, C, D* (Figure 24), *E.*
12*	**Pectis stenophylla** A. Gray var. **biaristata** (Rydb.) Keil **México.** SINALOA: 16.8 mi W of El Fuerte, *K & C 8752A, B, C* (Figure 25).
36	**Pectis subsquarrosa** (Hook. f.) Sch. Bip. **Galapagos Islands:** Hood Island, *C. H. Racine s.n.* (Figure 26).
24*	**Pectis swartziana** Less. **Honduras.** VALLE: 1.9 km S of jctn. w/CA–5 on CA–1, *K 9510A* (Figure 27), pop.
12*	**Pectis uniaristata** DC. var. **holostema** A. Gray **El Salvador.** LA LIBERTAD: 10.1 km N of Quetzaltepeque exit on El Salvador 1, *K 9452A, B.* **Honduras.** CHOLUTECA: 24 km W of Choluteca, *K 9512A* (Figure 28); 20 km W of Choluteca, *K 9515A.*

Table 2 — continued

Chromosome number (n)	Taxon with location and voucher
12*	**Pectis uniaristata** DC. var. **jangadensis** (S. Moore) Keil **México.** GUERRERO: 12 mi S of Chilpancingo, *K & C 9127* pop. JALISCO: 2.1 mi NW of Magdalena airport, *K & C 9004A, B;* 1.7 mi NW of jctn. w/México 70 on Mexico 15, *K & C 9024* pop. NAYARIT: 18 mi SE of Tepic, *K & C 8971-1* pop.; 16.3 mi W of Nayarit-Jalisco boundary on México 15, *K & C 8997A* (Figure 29), *B, D.*
12*	**Pectis angustifolia** Torr. var. **angustifolia** × **P. papposa** Harv. & Gray var. **grandis** Keil **United States.** TEXAS: Brewster Co.: Big Bend Natl Park, *K & M 7797;* Presidio Co.: 10 mi S of Cibola Creek, *K & M 7756* K^{d} (Figure 30), U^{g} (Figure 31).
12 II + 12 I*; 8 II + 20 I*	**Pectis bonplandiana** H. B. K. × **P. prostrata** Cav. **Guatemala.** SUCHITEPEQUEZ: Puente Siguacan *K & C 9438A, B* (Figure 32).
12*	**Pectis filipes** Harv. & Gray var. **filipes** × **P. papposa** Harv. & Gray var. **papposa** **México.** SONORA: 72 mi S of Benjamin Hill on Mexico 15. *K & C 8611D*[b] (Figure 33).
12*	**Pectis papposa** Harv. & Gray var. **papposa** × **P. sinaloensis** Fern. (*Pectis* × *salina* Brandeg.) **México.** SINALOA: Altata, *K & C 8786B, C, D* (Figure 34), *F.*
ca. 9 II + 18 I*	**Pectis swartziana** Less. × **P. uniaristata** DC. var. **holostema** A. Gray **Honduras.** CHOLUTECA: 20 km W of Choluteca, *K 9514B.*

*Previously unreported taxon or hybrid combination.

[a]Abbreviations of collectors' names: *K* = David Keil; *K & M* = Keil & Lyle A. McGill; *K & C* = Keil & Judith M. Canne. Voucher specimens are deposited at the Ohio State University Herbarium (OS).

[b]$2n$ = 12 II + 2 small supernumeraries.

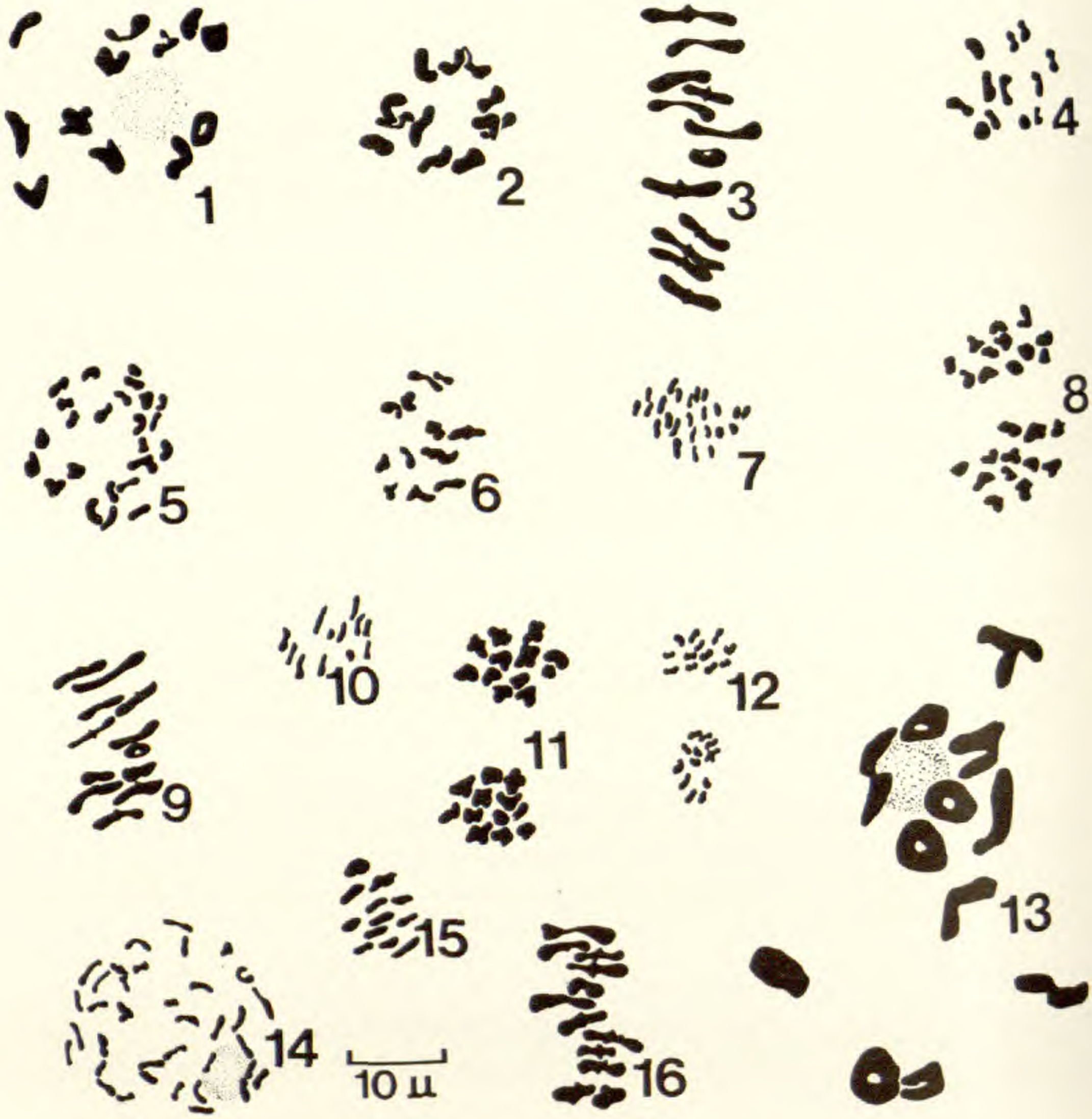
[c]Anaphase I bridge observed in some cells.

[d]Some cells contain one or two anaphase I bridges and associated fragments.

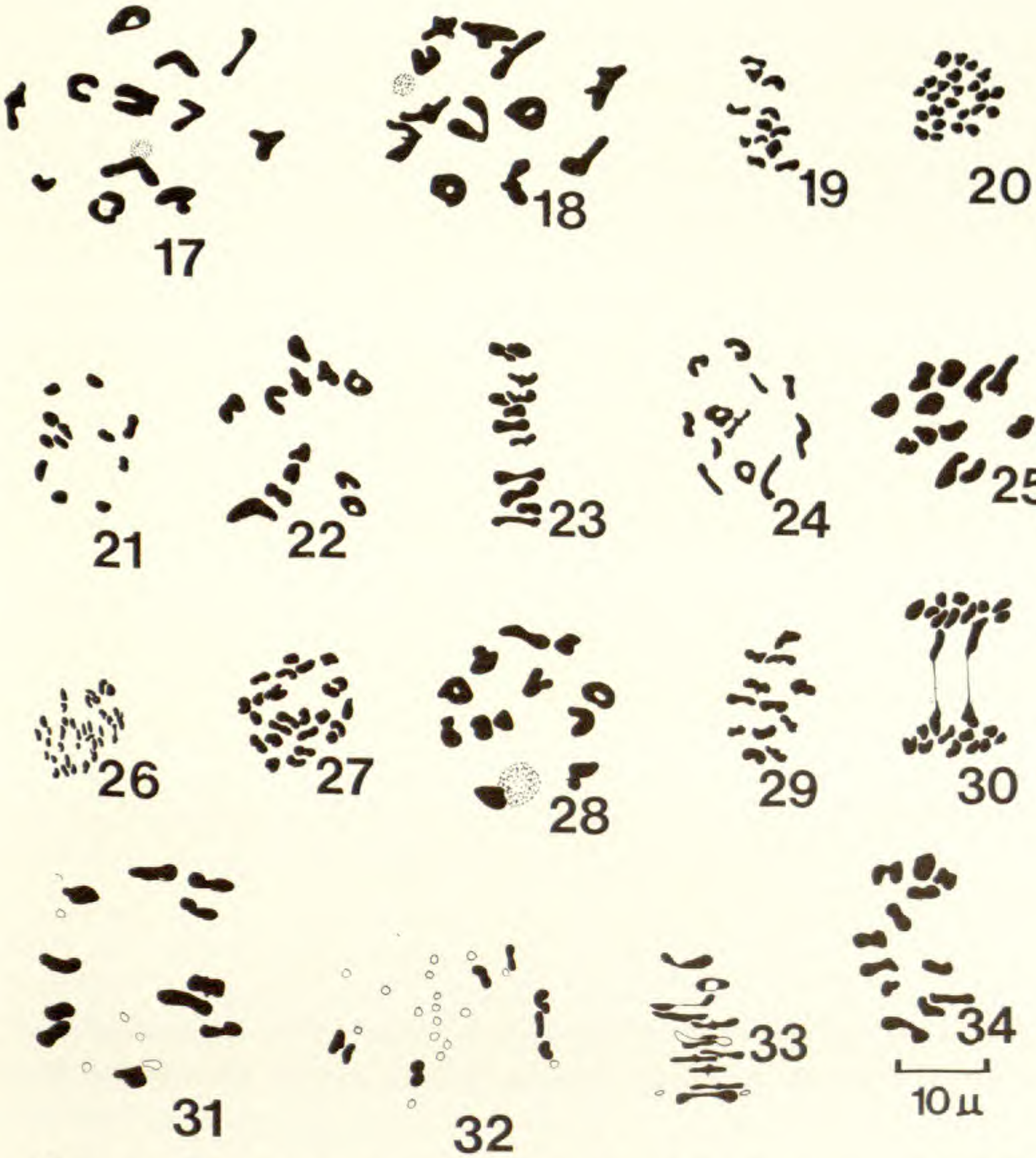
[e]$2n$ = 12 II + 1 small supernumerary.

[f]Some cells contained one or two anaphase I bridges and associated fragments. Synapsis in some cells resulted in formation of 10 II + 1 IV.

[g]$2n$ = 12 II + 6 small supernumeraries which synapsed irregularly; one pair of regular-sized chromosomes occasionally failed to synapse.



Figures 1–16. **Camera lucida drawings of meiotic chromosomes of Pectis taxa and hybrids.** Voucher specimens are cited in Table 2. All figures are the same scale. 1, *P. angustifolia* var. *angustifolia,* diakinesis, $2n = 12$ II. 2, *P. angustifolia* var. *fastigiata,* diakinesis, $2n = 12$ II. 3, *P. angustifolia* var. *tenella,* metaphase I, $2n = 12$ II. 4, *P. berlandieri,* metaphase I, $2n = 12$ II. 5, *P. bonplandiana,* diakinesis, $2n = 24$ II. 6, *P. capillipes,* metaphase I, $2n = 12$ II. 7, *P. cylindrica,* metaphase I, $2n = 24$ II. 8, *P. filipes* var. *filipes,* anaphase I, $n = 12$. 9, *P. filipes* var. *subnuda,* metaphase I, $2n = 12$ II. 10, *P. haenkeana,* metaphase I, $2n = 12$ II. 11, *P. incisifolia,* anaphase I, $n = 12$. 12, *P. leavenworthii,* telophase I, $n = 12$. 13, *P. longipes,* diakinesis, $2n = 12$ II. 14, *P. multifloscula,* diakinesis, $2n = 36$ II. 15, *P. oerstediana,* metaphase I, $2n = 12$ II. 16, *P. papposa* var. *papposa,* metaphase I, $2n = 12$ II.



Figures 17–34. **Camera lucida drawings of meiotic chromosomes of Pectis taxa and hybrids.** 17, *P. papposa* var. *grandis,* diakinesis, $2n = 12$ II. 18, *P. pringlei,* diakinesis, $2n = 12$ II. 19, *P. prostrata,* metaphase I, $2n = 12$ II. 20, *P. repens* metaphase I (polar view), $2n = 24$ II. 21, *P. repens,* diakinesis, $2n = 12$ II. 22, *P. rusbyi,* metaphase I, $2n = 12$ II. 23, *P. saturejaoides,* metaphase I, $2n = 12$ II. 24, *P. sinaloensis,* diakinesis, $2n = 12$ II. 25, *P. stenophylla* var. *biaristata,* metaphase I, $2n = 12$ II. 26, *P. subsquarrosa,* metaphase I, $2n = 36$ II. 27, *P. swartziana,* diakinesis, $2n = 24$ II. 28, *P. uniaristata* var. *holostema,* diakinesis, $2n = 12$ II. 29, *P. uniaristata* var. *jangadensis,* metaphase I, $2n = 12$ II. 30, *P. angustifolia* var. *angustifolia* × *P. papposa* var. *grandis,* anaphase I, $n = 12$, double inversion bridge plus fragments. 31, *P. angustifolia* var. *angustifolia* ×*P. papposa* var. *grandis,* metaphase I, $2n = 11$ II + 2 I + 6 supernumeraries. 32, *P. bonplandiana* × *P. prostrata,* metaphase I, $3n = 8$ II + 20 I (triploid). 33, *P. filipes* var. *filipes* × *P. papposa* var. *papposa,* metaphase I, $2n = 12$ II + 2 supernumeraries. 34, *P.* × *salina,* metaphase I, $2n = 12$ II.

possible translocation multivalent formations were found in a few individuals, but even in these individuals, not nearly all cells exhibited the irregularities. Based upon the low frequency of microsporocytes containing anaphase I bridges, it would appear that the inverted segments are relatively small and are not an effective isolating mechanism. Multivalents occur at an even lower frequency than bridges and likewise do not appear to be an effective barrier to hybrid fertility. Some hybrids possessed from one to six small supernumerary chromosomes which pair irregularly. These extra chromosomes were not limited to hybrids, however, as they occasionally appeared in non-hybrid plants as well.

Perhaps the most striking hybrid in sect. *Pectothrix* is *Pectis* × *salina,* a fertile hybrid between *P. papposa* var. *papposa* and *P. sinaloensis,* morphologically two very diverse parents. A well-developed hybrid swarm has formed where these two taxa grow together at Altata, Sinaloa. No evidence of chromosomal sterility barriers has been found in any members of this population. The two parents in this population are probably not very closely related, but apparently have retained ancestral chromosomal homology. The hybrid population has apparently been in existence for at least 70 years.

A distinctly different evolutionary line is represented by three species of the taxonomically difficult *Pectis elongata* complex: *P. berlandieri, P. oerstediana* and *P. uniaristata. Pectis oerstediana,* a Central American taxon, might better be treated as a variety of *P. elongata,* a South American species with which it has often been confused. Two varieties of *P. uniaristata* are reported here. One, var. *holostema* (*P. dichotoma* Klatt), is a predominantly Central American taxon. The other variety is one of those unusual taxa with an amphitropical distribution, with populations in west-central Mexico and in Southern Brazil. All the counts are from the Mexican range of the taxon. Recognition of the conspecificity of the Mexican and Brazilian population systems has necessitated the following new combination:

Pectis uniaristata DC. Prodr. **5:** 99. 1836. var. **jangadensis** (S. Moore) Keil, comb. nov. (Figure 35). BASIONYM: *Pectis jangadensis* S. Moore, Trans. Linn. Soc. London Bot. **4:** 389. 1895. TYPE: **Brazil.** MATO GROSSO: near Jangada, Sep 1891, *S. Moore 256* (Holotype: BM, not seen; isotypes, B, photo US!, K!, NY!).

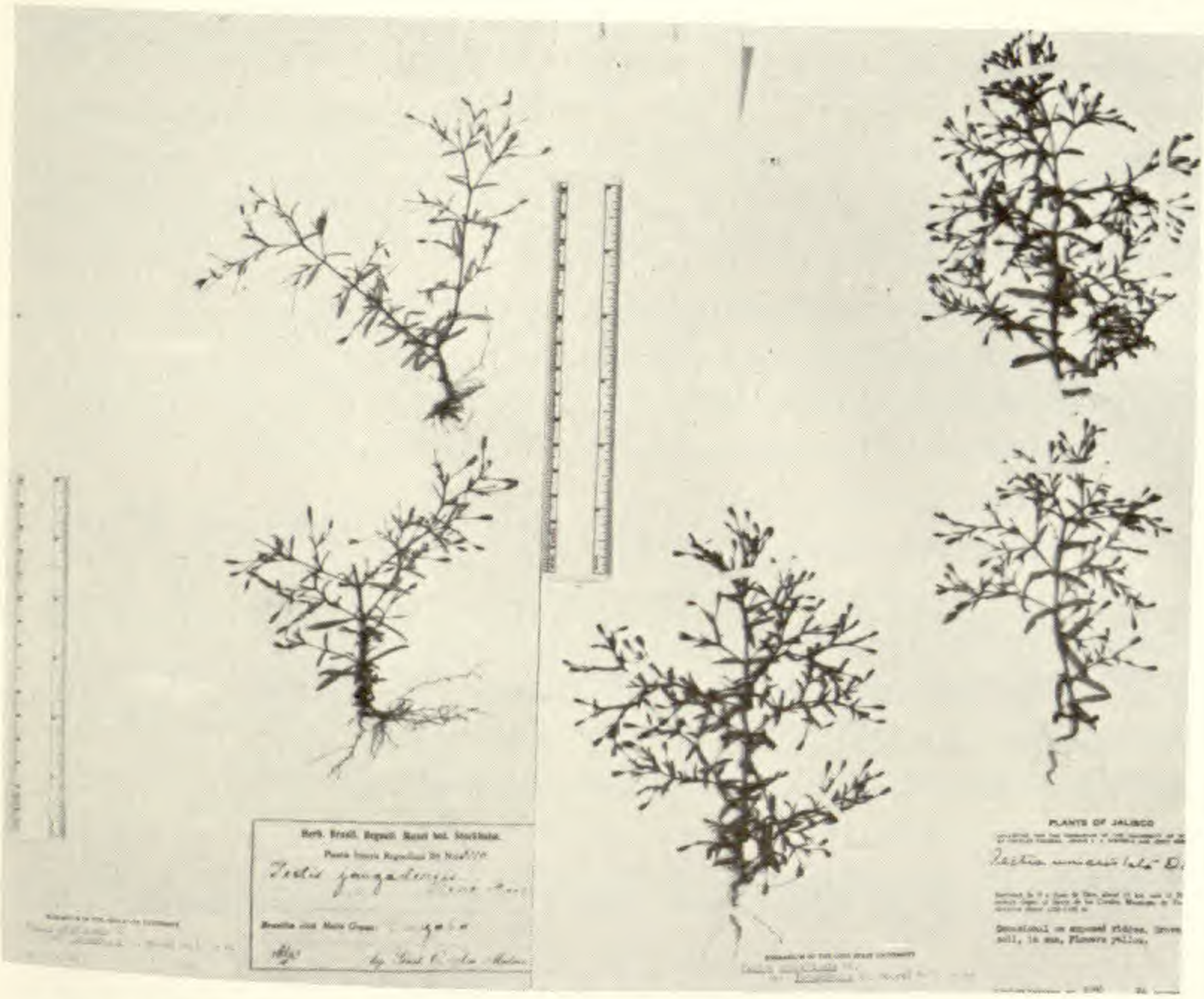


Figure 35. Brazilian and Mexican collections of *Pectis uniaristata* var. *jangadensis, Malme 3110* (GH) and *Feddema 2190* (MICH).

Typical *Pectis uniaristata,* also a Mexican taxon, has not yet been studied cytologically.

Stable polyploids have arisen in at least three different evolutionary lines in *Pectis.* Section *Lorentea* A. Gray, perhaps the most primitive of the genus, contains both diploids and polyploids. Three species from the section, *P. haenkeana, P. leavenworthii* and *P. saturejaoides,* are known only as diploids, and one, *P. latisquama,* has been reported only at the tetraploid level. *Pectis repens,* also a member of sect. *Lorentea,* apparently has both diploid and tetraploid races. Further study of additional populations will be necessary for an understanding of the basis for these different races. The two levels may eventually prove to represent cryptically differing species. *Pectis multiflosculosa,* a widespread perennial species which occurs on Pacific Ocean beaches from Sinaloa to Peru, is one of the two known hexaploids

in the genus. This unusual species, unique in its long-creeping habit, may be a member of sect. *Lorentea*.

Section *Pectis* is represented at both the diploid and the tetraploid levels. The discovery that *Pectis prostrata* is a diploid whereas the very similar *P. cylindrica* is a tetraploid adds considerable weight to the argument that the two should be treated as distinct species (Keil, 1975A). *Pectis bonplandiana* and *P. swartziana*, two closely related and very similar species (Keil, 1974), are both tetraploids. Further study may indicate that these two taxa are actually conspecific.

Two triploids, both the result of diploid-tetraploid hybrids, represent the first reports of this polyploid level in *Pectis*. In both hybrids, *P. bonplandiana* × *P. prostrata* and *P. swartziana* × *P. uniaristata*, partial pairing occurred, indicating at least some homology or homoeology of the parent chromosome complements. The evidence is insufficient, however, to indicate that the diploids involved in these hybrids are directly involved in the ancestry of the respective tetraploids. As was indicated above, evolution in some parts of *Pectis* has not been accompanied by chromosomal isolation, and the chromosomes of quite different species may be capable of full pairing. The ability of *P. uniaristata* var. *holostema* to hybridize with a member of sect. *Pectis* suggests that there may be a fairly close relationship between the *P. elongata* complex and sect. *Pectis*.

The only species known cytologically from the South American region is *Pectis subsquarrosa*, a hexaploid endemic of the Galapagos Islands. The hexaploid level suggests that this species has had a complex evolutionary history. Current research (Keil, unpubl.) suggests that a pattern of adaptive radiation and subsequent migration may have played a part in the evolution of both *P. subsquarrosa* and *P. tenuifolia* (DC.) Sch. Bip., also endemic to the Galapagos Islands. Further samples of these species from additional islands may provide more information regarding the evolution of these species. Both Galapagos Islands species are members of an unnamed South American section of *Pectis*.

Diploid counts are reported here for the first time for two perennial species of uncertain affinities. *Pectis longipes* appears to be most closely related to sect. *Pectothrix* but also possesses features in common with some members of sect. *Lorentea*. *Pectis*

capillipes (*P. erecta* Fern.) appears to be most closely related to members of the *P. elongata* complex, perhaps through the perennial *P. diffusa* Hook. & Arn.

Thirty-four taxa in *Pectis* are now known cytologically, some from many populations, some from only one. Thus far, only one base number, $x = 12$, has been reported for the genus. This situation is in strong contrast to that found in the other large genera of the Tageteae, which are all multibasic: *Dyssodia*, $x = 7,8,(12?),13$ (Johnston & Turner, 1962; Strother, 1969); *Porophyllum*, $x = 11, 12, 15$ (Johnson, 1969); and *Tagetes*, $x = 11,12$ (Strother, 1969). In light of the variability of the chromosome numbers of these related genera, it is surprising that such a widespread and diverse genus as *Pectis* has remained monobasic. Certainly not all of the taxa of *Pectis* have been examined cytologically, and the possibility still exists that additional base numbers may yet be discovered. The probability of such an event is lessened, however, by the broad spectrum of the genus which has now been sampled.

The largest gaps in the present knowledge of the cytology of *Pectis* lie in the West Indian and South American range of the genus. Of particular value will be counts from additional members of sect. *Pectis*, particularly from the Caribbean region.

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DEPARTMENT OF BOTANY
THE OHIO STATE UNIVERSITY
1735 NEIL AVENUE
COLUMBUS, OHIO 43210

Present Address:
BIOLOGICAL SCIENCES DEPARTMENT
CALIFORNIA POLYTECHNIC STATE UNIVERSITY
SAN LUIS OBISPO, CALIFORNIA 93407

CYTOGEOGRAPHY OF SEDUM LANCEOLATUM AND ITS RELATIVES

CHARLES H. UHL

Some species of *Sedum* that are widely distributed in the United States have two or more chromosome races. In several species these races differ by simple polyploidy, e.g., $n = 8$, 16 and 24 in *S. ternatum* Michx. (Baldwin, 1943; Uhl, 1970); $n = 12$, 24, 36 and 48 in *S. wrightii* A. Gray (Uhl, 1972). In other species the chromosome races differ in other ways, e.g., $n = 14$ and 22 in *S. glaucophyllum* Clausen (Uhl, 1970); $n = 14$, 15 and 16 in *S. cockerellii* Britton (Uhl, 1972). Two patterns of numerical variation have been described (Uhl, 1972): one, called "casual variation," in which occasional plants (usually trisomics and plants with B-chromosomes) differ from others of the same population, and the other, called "established variation," in which plants of some populations consistently differ from plants of other populations in their chromosome numbers. Presumably, established variants originated as casual variants whose karyotypes became fixed in their populations.

This paper is part of a general survey of the cytotaxonomy of the Crassulaceae in the United States and Mexico. It reports the chromosome numbers of about 320 collections, representing a broad geographical sample, of nine yellow-flowered species of *Sedum* that are native to the western United States and Canada. The classification follows Clausen (1975), who has made a detailed taxonomic study of all of these species and has published chromosome counts of about 40 collections, including a dozen of those reported here. In eight of the species the basic karyotype clearly consists of 8 chromosomes that are rather large compared to those of most other species of *Sedum*, and these species are considered to represent a single natural group (Clausen, 1975). The ninth species, *S. oreganum* Nuttall ($n = 12$), seems relatively isolated both cytologically and taxonomically. The data allow some observations regarding the probable role of polyploidy in evolution of these species.

Collections were made and studied sporadically over a period of more than 20 years. Buds were fixed in modified Carnoy's solution (3 parts chloroform, 2 parts absolute ethanol, 1 part

glacial acetic acid) sometimes directly from plants in the wild, more often from field-collected plants in cultivation. A few seemingly discrepant counts should probably be checked, since it is possible, despite all precautions, that rodents or sparrows might have mixed some plants cultivated in the cold frame. Anthers were squashed in acetocarmine, the chromosomes were studied at meiosis in pollen-mother cells, and the slides were made permanent. Most herbarium vouchers are in the Wiegand Herbarium or the Bailey Hortorium of Cornell University; some are at the University of California, Berkeley, where part of this study was conducted. Thanks are extended to the many persons who contributed collections and expecially to Mrs. Margaret Evans of Reno, Nevada, who provided a number of collections from remote localities.

Collections studied are listed in Appendix 1, arranged approximately from north to south and from west to east. Except as indicated by asterisks, only one plant of a collection was studied.

Sedum lanceolatum Torrey is listed as *S. stenopetalum* Pursh in many floras (see Clausen, 1948). It is by far the most widely distributed of the species, ranging from Alaska to the Black Hills of South Dakota and south to the southern Sierra Nevada of California, northern Arizona and New Mexico. It is most often found on granitic rocks and on their outwash, and it appears to be scarce, or probably absent, from lavas and basalt, as in the southern part of the Cascade Range and on the Columbia Plateau. Diploids ($n = 8$), tetraploids ($n = 16$) and hexaploids ($n = 24$) occur, mostly or entirely as established variants. Each level of ploidy is widespread (Figure 1) and exhibits considerable morphological diversity. No obvious morphological characters allow plants with one level of ploidy to be consistently distinguished from those with the others. It seems likely that polyploidy has evolved within the species more than once.

Diploid *Sedum lanceolatum* ($n = 8$, Figure 2) was found at 71 localities: in the eastern Canadian Rockies, in Glacier Park, in the Uinta Mountains of Utah, in the Front Range of the Colorado Rockies, on summits in the Klamath Mountains of southwestern Orgeon and northwestern California, and scattered elsewhere. In elevation it ranges from alpine tundra above 3700 meters (e.g., Trail Ridge in Rocky Mountain National Park) down to the level of the western Great Plains (e.g., vicinity

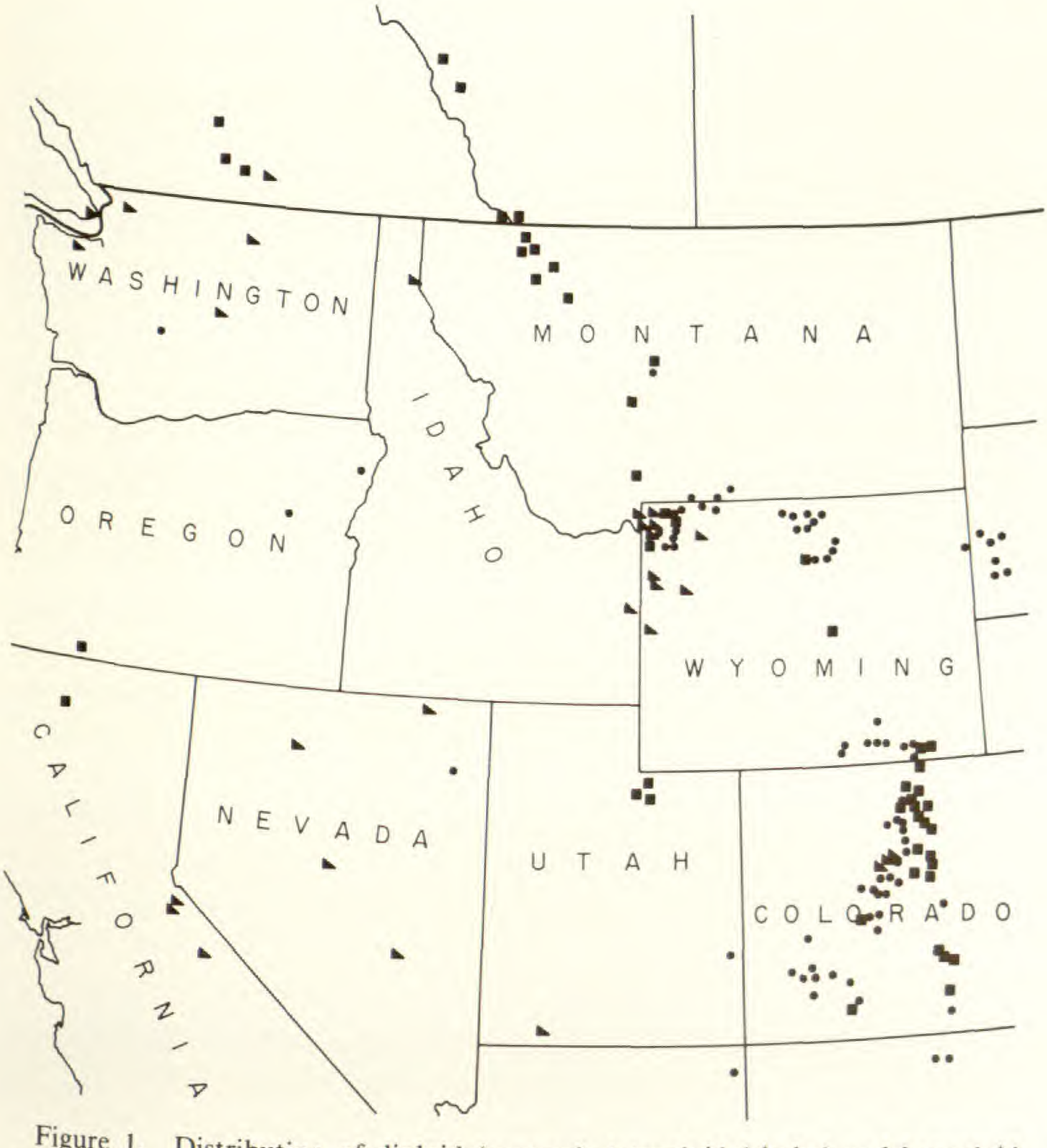
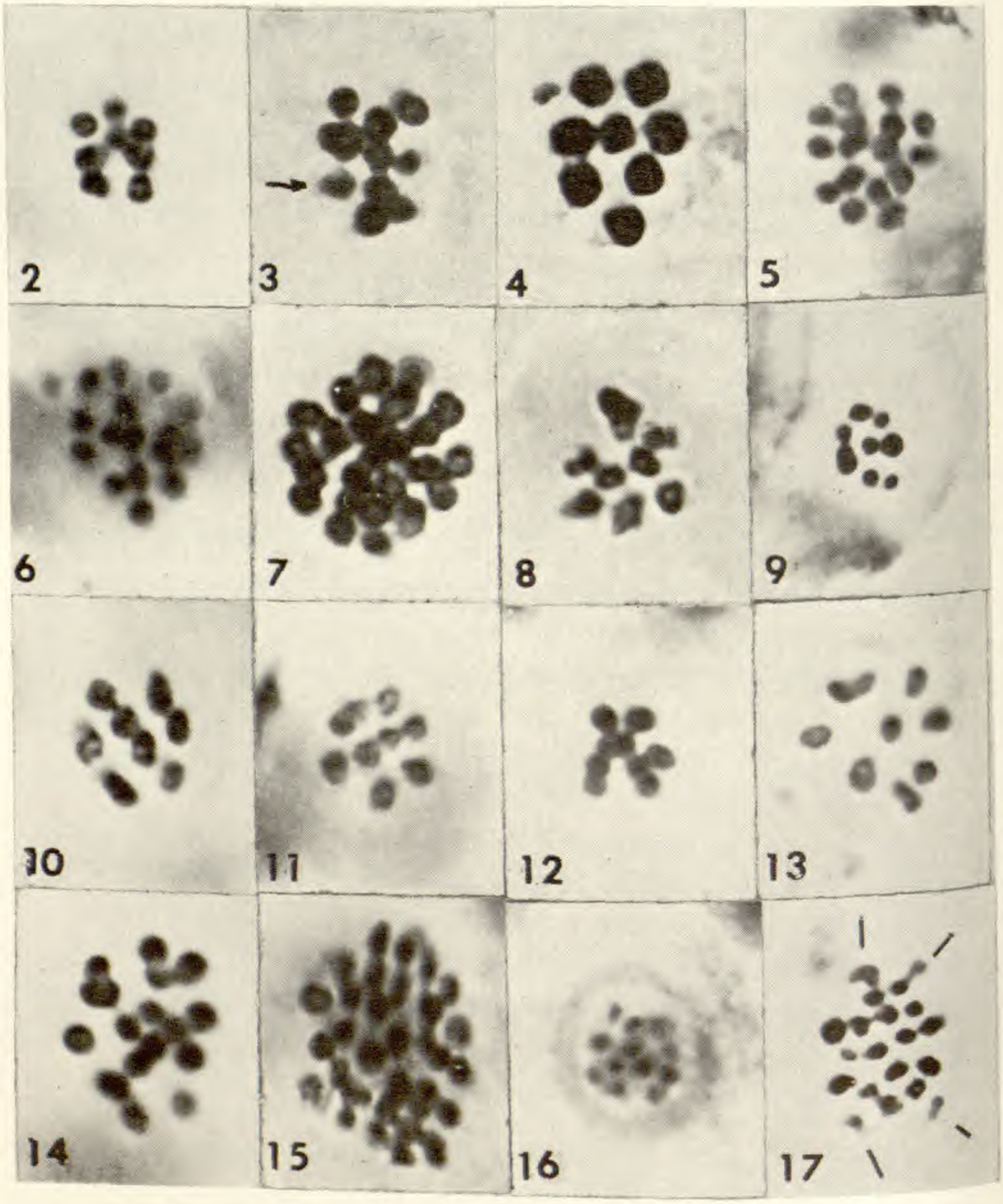


Figure 1. Distribution of diploid (squares), tetraploid (circles) and hexaploid (triangles) plants of *Sedum lanceolatum* in the western United States and Canada. In some areas all collections are not indicated.

of Boulder and Denver, Colorado) and still lower farther north. Three casual variants were found: one apparent trisomic, a polysomic (Figure 3, see below) and one plant with a small B-chromosome (Figure 4).

Tetraploid *Sedum lanceolatum* ($n = 16$, Figure 5) was found at 107 localities: in the Black Hills of South Dakota, in the Bighorn, Beartooth, Medicine Bow, and Sherman Mountains, and in the eastern part of Yellowstone Park, all in Wyoming, in most of Colorado west of the crest of the Front Range, in



Figures 2–17. Chromosomes of *Sedum* at metaphase I in pollen-mother cells, ×2000. 2–7, *S. lanceolatum:* 2, *U400*, $n = 8$; 3, *U2208A*, $n = 9 + 1$ (arrow indicates univalent; one bivalent is not in good focus); 4, *U1954*, $n = 8 + 1B$; 5, *U405*, $n = 16$; 6, *U1715*, $n = 16 + 1B$; 7, *U974*, $n = 24$. 8, *S. debile, U1059*, $n = 8$. 9, *S. divergens, U1183*, $n = 8$. 10, *S. leibergii, U1035*, $n = 8$. 11, *S. radiatum* ssp. *radiatum, U903*, $n = 8$. 12, *S. radiatum* ssp. *ciliosum, U944*, $n = 8$. 13, *S. radiatum* ssp. *depauperatum, UC62.1115*, $n = 8$. 14, *S. rupicolum, U1040*, $n = 16$. 15, *S. stenopetalum, U1046*, $n = 32$. 16, *S. oreganum, U383*, $n = 12$. 17, *S. borschii, C42–31*, pentaploid, with 16 bivalents and trivalents (most of them having a more "solid" appearance here because of their greater depth of focus) and 4 univalents, indicated by lines, around the edges of the plate.

eastern Oregon, in northern Arizona and New Mexico, and scattered elsewhere. It occurs in alpine tundra in the Beartooth Mountains of northwestern Wyoming and at several places in Colorado (e.g., Loveland Pass, 3650 meters). It is also abundant at lower elevations with sagebrush on gravelly outwash deposits in Middle Park (Grand County, Colorado) and elsewhere. Two casual variants, one probable trisomic and another with a large B-chromosome (Figure 6), were found.

Hexaploid *Sedum lanceolatum* ($n = 24$, Figure 7) was found at 40 localities: in the Sierra Nevada of California, on several isolated ranges in Nevada, in southwestern Utah (Zion Park), at sea level around northern Puget Sound and adjacent waters, in the Okanogan Valley and Wenatchee Mountains of south central British Columbia south to central Washington, in western Yellowstone Park and the Grand Tetons, and in a small area of the Gore Range in central Colorado. On the basis of herbarium records, the species appears to be common in the high Sierra Nevada, and hexaploids probably occur there above timberline. Clearly, each level of ploidy is represented at a wide range of elevations, and no relationship of ploidy to elevation is detectable. Clausen's (1975) reports of counts from 10 other scattered localities mostly conform to the distributions of the chromosome races found in the much larger sample reported here.

Some areas appear to have only one chromosome race of *Sedum lanceolatum,* but others have more. Only diploids were found in the eastern Canadian Rockies (4 localities) south through the vicinity of Glacier Park, Montana (6 localities). The northern part of the Front Range in Colorado to south of Denver seems to be populated only by diploids from the crest eastward (35 localities), but tetraploids are found just west of the crest and also just south of Pikes Peak. To the north, the eroded Sherman Mountains (southern Laramie Mountains) also have diploids in the east (5 localities), and tetraploids to the west (6 localities). Although some samples are small, the Uinta Mountains appear to be populated only by diploids (4 localities), the Black Hills (13 localities, including 9 collections of Professor R. T. Clausen not listed in Appendix 1) and Medicine Bow Mountains (6 localities) appear to have only tetraploids, and the Grand Tetons (3 localities) and Sierra Nevada (3 localities)

only hexaploids. Samples from other mountain ranges are either too small or mixed in their ploidy.

In several areas, collections of different levels of ploidy were made within short distances of one another. However, most of these cases seem to correspond to boundaries between chromosome races, and it is not clear how much mixing, if any, occurs within the same population. Southeast of Vail Pass in central Colorado a tetraploid (*U2276*) was found less than a kilometer from a hexaploid (*U1710*). Six other hexaploid collections were made within about 16 km. of this locality, and the nearest other tetraploid came from about 10 km. away. From the Fall River road in Rocky Mountain National Park, a plant was found (*U2208A*), along with two normal diploids (*U2208B, U2208C*), which formed 9 bivalents and a univalent at metaphase I (Figure 3). Presumably this polysomic plant descended from a diploid-tetraploid hybrid. The nearest known locality for a tetraploid is at Milner Pass, about 10 km. west.

All three chromosome races of *Sedum lanceolatum* occur in Yellowstone Park. In the eastern part of the park 12 collections in the valley of the Yellowstone River and its tributaries were tetraploid, and two were diploid. In the western part 13 hexaploid collections came from Mammoth Hot Springs south into the valley of the Madison River and its tributaries, along with one tetraploid and one diploid. Plants collected in 1969 and 1973 from rocks on the hill overlooking Old Faithful were hexaploid, whereas on decomposing geyserite near Giantess Geyser, less than 400 meters to the west, the collection (*U1052*) was diploid. In the Big Horn Mountains of Wyoming, 15 collections were tetraploid, with a single diploid found in Tensleep Canyon about 6 km. below the nearest tetraploid. In the Little Belt Mountains of central Montana a collection at Kings Hill Pass was tetraploid, but another collection 10 km. north was diploid. Some other scattered cases of different levels of ploidy were found in nearby collections, and doubtless further study would reveal more.

Clausen (1975) recognized three subspecies of *Sedum lanceolatum,* chiefly on the basis of plant size. The largest, subsp. *nesioticum* (G. N. Jones) Clausen, occurs near sea level in the vicinity of Puget Sound and the Strait of Georgia, and both populations studied were hexaploid ($n = 24$). The diminutive subsp. *subalpinum* (Blankinship) Clausen is adapted to the brief

growing season of timberline and above. However, it intergrades with the larger subsp. *lanceolatum,* and Clausen (1975, p. 231) considered it "at an evolutionary stage somewhere between ecotype and subspecies." These two subspecies are not distinct cytologically and are listed together in Appendix 1. On Trail Ridge in Rocky Mountain National Park diminutive plants near timberline are diploid ($n = 8$), but in the Beartooth Mountains, northeast of Yellowstone Park, similar plants are tetraploid. Most collections clearly belong to the wide-ranging, intermediate-sized subsp. *lanceolatum,* which includes diploids, tetraploids and hexaploids.

The type collection of *Sedum lanceolatum* was made by Dr. E. P. James, an army surgeon who was also botanist and geologist for the expedition to the Rocky Mountains led by Major Stephen H. Long in 1820 (Torrey, 1828). During two weeks in July of that year the expedition explored the eastern base of the Front Range, roughly from the present sites of Denver to Pueblo, Colorado (Fuller & Hafen, 1957). On July 13 and 14, James and two companions made the first recorded ascent of Pikes Peak, collecting plants along the way and traversing a region just below timberline where ". . . the yellow flowered stone-crop (*Sedum stenopetalum,* Ph.) [surely *S. lanceolatum*] is almost the only herbaceous plant which occurs" (James, 1823, vol. II: 26–27). Although no plants from Pikes Peak itself have been studied cytologically, two collections from 7 and 11 km. south of its summit (*U2280, U2281*) are tetraploid ($n = 16$). However, to the north all collections from the crest of the Front Range eastward are diploid. Clausen considered that plants from East Plum Creek, about 50 km. north of Pikes Peak near Larkspur, Colorado, are "reasonable topotypes" and reported that they are diploid ($n = 8$), but the ploidy of the type collection must still be regarded as uncertain. Study of the size of the pollen grains or stomatal guard cells might determine this definitely.

Sedum borschii Clausen, endemic to Idaho and western Montana, was recently (1975) elevated from varietal status under *S. leibergii.* At metaphase I the lone plant studied here usually produced 16 bivalents and multivalents plus a variable number of univalents in different cells (Figure 17) and often had a laggard or two and sometimes a bridge at anaphase I. Metaphase II plates had 17–23 elements, with 18 and 22 observed on the two plates in

one cell and 17–1–22 in another. This means that the somatic chromosome number must have been 40 and that the plant was pentaploid. Many microspore quartets included a small extra spore. Clausen (1975) also reported meiotic irregularities and/or differing and uncertain counts but "guessed" that the species is usually hexaploid, with $n = 24$. He considered vegetative reproduction to be important in the species but thought some functional seeds were produced. He also speculated about possible origin of the species as an allopolyploid hybrid between *S. leibergii* and *S. stenopetalum* and/or *S. lanceolatum*. The chromosome number and behavior reported here are compatible with origin of *S. borschii* as a hybrid between octoploid *S. stenopetalum* ($n = 32$) and diploid *S. leibergii* ($n = 8$). The possibility that this species is a hybrid maintaining itself by asexual means needs further study.

Sedum debile S. Wats. is native chiefly to mountains of the Great Basin and adjacent areas to the north and east, from western Wyoming to Nevada and eastern Oregon. All 9 collections studied were diploid, $n = 8$, with one metacentric bivalent conspicuously larger than the others (Figure 8). The karyotype at meiotic metaphase appears constant in number and form. Clausen (1975) reported $n = 8$ for plants from three localities in the Grand Tetons.

Sedum divergens S. Wats., like the preceding, has decussate leaves, but at maturity its carpels are spreading rather than erect. It occurs in the Cascade and Olympic Mountains from west central Oregon well north into British Columbia, with one or two isolated populations in the Klamath Mountains (Clausen, 1975). All 6 collections studied had $n = 8$, also with one bivalent larger than the others, but a bit less conspicuously so than in the preceding taxon (Figure 9). The meiotic chromosomes of *S. divergens* and *S. debile* appear very similar, and probably these two species are more closely related to each other than either is to any other species of *Sedum*. Clausen (1975) reported $2n = 16$ for plants from a locality near Mount Baker, Washington, and another in the Wenatchee Mountains of central Washington, and Taylor and Mulligan (1968) reported $n = 8$ for plants from two localities in the Queen Charlotte Islands of British Columbia.

Sedum leibergii Britton is a small, often biennial species occurring chiefly on basalts of the Columbia Plateau. After flowering

it may die completely, or it may perennate by tiny lateral buds from the base of the inflorescence. Seven collections studied were all diploid ($n = 8$, Figure 10), and no prominent differences in size among the bivalents at meiosis were noted.

Sedum radiatum Watson and *S. ciliosum* Howell were previously classified as subspecies of the otherwise octoploid *S. stenopetalum* (Clausen, 1948). However, both are diploid ($n = 8$), and because of the differences in levels of ploidy and in some morphological characters, as well as their annual habit (though often perennating by lateral buds), Clausen (1975) now recognizes *S. radiatum* as a separate species with three subspecies. *Sedum radiatum* subsp. *radiatum* ($n = 8$, Figure 11; 16 collections studied) occurs chiefly in the California Coast Ranges, with a few outlying populations in the southern Sierra Nevada and in the southern Klamath Mountains. To the north, in the central Klamath (Siskiyou) Mountains along the California-Oregon border, it is replaced by the newly described subsp. *depauperatum* Clausen ($n = 8$, Figure 13; 3 collections studied). Still farther north, subsp. *ciliosum* (Howell) Clausen ($n = 8$, Figure 12; 5 collections studied) is limited to southwestern Oregon in the northern Klamath Mountains and in the Coast Ranges. One larger metacentric bivalent is usually noted in all three subspecies (Figures 11–13), which have karyotypes similar to those of *S. debile* (Figure 8) and *S. divergens* (Figure 9).

Sedum rupicolum G. N. Jones occurs in the northern Cascades and in the Wenatchee Mountains of central Washington, often on serpentine (Clausen, 1975). Both collections studied, one possibly from the type clone, were tetraploid ($n = 16$, Figure 14) and not distinguishable cytologically from tetraploid *S. lanceolatum* (Figure 5). This species does not seem much more distinct than certain other variants of *S. lanceolatum*, and it has previously been reduced to infraspecific status (Hitchcock & Cronquist, 1964).

The type collection of *Sedum stenopetalum* was made in western Montana in 1806 by members of the Lewis and Clark expedition. Clausen (1948) reported that the type specimen also includes material of *S. lanceolatum* (which was later described accurately by Torrey in 1828), but Pursh's 1814 description of compressed subulate leaves and linear petals applies only to the former species. In 1840, W. J. Hooker recognized the existence

of two species, but he applied Pursh's name to the wrong element and redescribed *S. stenopetalum* as *S. douglasii* (Clausen, 1948). Unfortunately, Hooker's usage became standard for many years and was common in manuals and floras until only recently.

Sedum stenopetalum (*S. douglasii* of many floras) occurs from southern British Columbia and western Montana to California. Its typical subspecies is consistently octoploid ($n = 32$, Figure 15; 32 collections). Some scattered populations, subsp. *monanthum* (Suksdorf) Clausen, are made up mostly or completely of plants with single-flowered inflorescences; moreover, the flowers are paler yellow. These also are octoploid (5 collections). Clausen (1975) reported that the species is octoploid, or approximately so, at four additional localities.

Sedum oreganum Nuttall occurs in the Cascade Mountains and Coast Ranges from Oregon north to southern Alaska. It somewhat resembles *S. divergens* and was collected with that species at several places, e.g., Keechelus Lake (east of Snoqualmie Pass, Washington) and Tombstone Pass (Linn County, Oregon), but its leaves are flatter and not decussate, and its petals are connate basally. Plants of 15 collections made from southern British Columbia to the central Oregon coast all had $n = 12$ (Figure 16), as did plants from five other localities reported by Clausen (1975). This species is sometimes classed with *Sedum* subg. *Gormania* (Clausen, 1975), but all other species of that group have strictly $n = 15$ or a multiple of that number (Clausen & Uhl, 1944; Clausen, 1975; Uhl, unpublished). Thus, *S. oreganum* seems to be isolated cytologically, fitting into neither the *Gormania* group ($x = 15$) nor the *lanceolatum* group ($x = 8$), both of which are strictly euploid with different chromosome numbers.

Clausen (1975) recognized two subspecies of *Sedum oreganum*. The larger subsp. *oreganum* occurs along the coast and in the Coast Ranges, and the slightly smaller subsp. *tenue* Clausen is endemic to the Cascade Mountains. Their chromosomes appear the same.

Polyploidy appears to be a very important isolating mechanism among these species. With only two apparent exceptions known, species of the *Sedum lanceolatum* group are always of different levels of ploidy where they occur together. Thus, *S. stenopetalum* ($n = 32$) occurs with diploid *S. lanceolatum* ($n = 8$) at several places in the vicinity of Glacier National Park, Montana, (*U398*

& *U399; U1197* & *U1198; U1804* & *U1805*) and adjacent Waterton Lakes National Park, Alberta (*U393* & *U394*), and doubtless elsewhere. It occurs with tetraploid *S. lanceolatum* ($n = 16$) in the Blue Mountains (*U1189* & *U1190*) and Wallowa Mountains (*U1565* & *U1566*) of northeastern Oregon, with hexaploid *S. lanceolatum* ($n = 24$) in southern British Columbia (*U1812* & *U1813*), and in Jackson Hole, Wyoming (Clausen, 1975), and near the latter in north central Washington (*U1956* & *U1957*). *Sedum stenopetalum* ($n = 32$, *U1041,* mostly one-flowered) occurs with *S. rupicolum* ($n = 16$, *U1040*) and at least near hexaploid *S. lanceolatum* ($n = 24$, *U1814*) in the Wenatchee Mountains of Washington, where Clausen (1975) has reported the presence also of diploid *S. divergens* ($n = 8$). *Sedum stenopetalum* subsp. *monanthum* ($n = 32$, *U1212*) occurs with *S. radiatum* subsp. *depauperatum* ($n = 8$, *U1213*) on Copper Butte in the Siskiyou Mountains of northern California.

Hexaploid *Sedum lanceolatum* ($n = 24$, *U1053*) occurs with octoploid *S. stenopetalum* ($n = 32$) (Clausen, 1975) and with *S. debile* ($n = 8$, *U1054*) in the Grand Teton Mountains and/or Jackson Hole, Wyoming, near *S. debile* in Zion National Park, Utah (*U1160* & *U1159*), and probably with *S. debile* in the Quinn Canyon (*U1302*) and Jarbridge Mountains (*U1225*) of Nevada. However, plants of *S. debile* from these last two locations died before counts could be obtained. Tetraploid *S. lanceolatum* ($n = 16$, *U1223*) occurs with *S. debile* (not counted) in the East Humboldt Range of Nevada.

Two apparent exceptions are known to the rule that species of this group occurring together are of different levels of ploidy. In the Uinta Mountains of northern Utah diploid *Sedum lanceolatum* ($n = 8$, *U1985–U1988*) and *S. debile* ($n = 8$, *U1990, U1991*) both occur and flower at the same time. Unfortunately, plants of one or the other of the two species collected together there died before counts could be made. Clausen (1975) reported tetraploid *S. lanceolatum* ($n = 16$) from the Wenatchee Mountains in close proximity to *S. rupicolum* ($n = 16$), but my only count of *S. lanceolatum* from this area is hexaploid ($n = 24$, *U1814*).

The only aneuploids encountered were three probable polysomics and two plants with B-chromosomes (Figures 3, 4, & 6),

all in *Sedum lanceolatum*. All clearly were casual variants, and aneuploidy has played no detectable role in evolution among these species. The only established variants found are polyploids, also in *S. lanceolatum*. In this species ploidy often appears to vary as an adjustment that favors its separate coexistence in proximity with other members of the group having a different level of ploidy. All other species, with the possible exception of *S. borschii,* are homogeneous in their ploidy.

At meiosis some polyploids exhibit probable multivalents and close secondary associations of bivalents, phenomena that suggest autopolyploidy. Compared to the diploids, the polyploids of *Sedum lanceolatum* show no greater resemblance to any other species, as would be expected if they were allopolyploids. *Sedum stenopetalum* is always octoploid, and one can only guess at its diploid progenitor(s).

Clausen (1975) reported that natural hybrids occur between *Sedum stenopetalum* and *S. lanceolatum* in Jackson Hole, Wyoming, and in the Wenatchee Mountains of central Washington. However, in seven of eight morphological characters in his table (p. 281) the presumed hybrid closely resembles or transcends *S. lanceolatum* and shows no influence at all of *S. stenopetalum*. *Sedum stenopetalum* is always octoploid ($n = 32$), whereas *S. lanceolatum* is hexaploid ($n = 24$) in Jackson Hole and tetraploid and/or hexaploid in the Wenatchee Mountains. Thus, first-generation hybrids in Jackson Hole would be expected to be heptaploids with $2n = 56$, and Clausen's hybrids are reported to have $2n = 50$–59. He also reported and described a single natural hybrid between *S. stenopetalum* and *S. borschii* and mentioned possible hybrids of *S. lanceolatum* with *S. rupicolum* and *S. divergens*.

The Klamath Mountains of southwestern Oregon and northwestern California are populated by octoploid plants of *Sedum stenopetalum* and five different diploids: *S. lanceolatum* (on mountain tops), all three subspecies of *S. radiatum,* and, according to Clausen (1975), two relictual populations of *S. divergens*. Apparently, none of the diploids occur together in this region. The principal distribution of *S. divergens* is contiguous to the north, and the ranges of the other two diploids, *S. leibergii* and *S. debile,* are contiguous to the northeast and east, respectively.

Sedum oreganum ($n = 12$) also occurs just north of this area, which is also a center of diversity for *Sedum* subg. *Gormania* (Clausen & Uhl, 1944). Whittaker (1960) pointed out that the Klamath region is geologically old, very diverse in climate and soils, and bears an old and very diverse flora. He considered it to be a "center" for forest floras of the West. It also may well have been the center of origin for the species considered here.

SUMMARY

Eight yellow-flowered species of *Sedum* of the western United States, *S. lanceolatum, S. borschii, S. debile, S. divergens, S. leibergii, S. radiatum, S. rupicolum,* and *S. stenopetalum,* all have a basic chromosome number of 8 and are believed to comprise a natural group. A ninth species, *S. oreganum,* is cytologically distinct with $n = 12$, and it seems taxonomically more isolated. *Sedum lanceolatum* includes widespread diploids, tetraploids and hexaploids. *Sedum rupicolum* is tetraploid, *S. stenopetalum* is octoploid, and *S. borschii* is often (always?) irregular at meiosis and may be a polyploid hybrid. All the remaining species are diploid. Polyploidy seems to be an important isolating mechanism between taxa when plants of two or more of these species occur together.

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DIVISION OF BIOLOGY
CORNELL UNIVERSITY
ITHACA, N. Y. 14853

APPENDIX I. COLLECTIONS STUDIED

Sedum borschii Clausen. ($2n$ = 40, meiosis irregular.)

Montana. MISSOULA COUNTY: Rattlesnake Valley, NE of Missoula (*F. N. Rose*) (*C42-31*).

Sedum debile S. Wats. (n = 8.)

Nevada. ELKO COUNTY: Lamoille Canyon, Ruby Mtns., 8000′ (*M. Williams*) (*U1072*). NYE COUNTY: Pine Cr., E side of Mt. Jefferson, Toquima Range, 7800′ (*M. Williams*) (*U1561*). **Utah.** CACHE COUNTY: Upper Logan Canyon, Wasatch Range, 13 mi. W of Garden City (*U1058*); Logan Canyon, 18 mi. NE of Logan (*U1059*). WASATCH COUNTY: Daniels Canyon, Wasatch Range, 11 mi. SE of Heber (*U1063*). SUMMIT COUNTY: Uinta Mtns., Stillwater Campground, 46 mi. NE of Kamas, 8600′ (*U1991*); 9 mi. N of Mirror Lake, 9100′ (*U1990*). WASHINGTON COUNTY: Hidden Canyon, Zion National Park, 5200′ (*U1159*). **Wyoming.** TETON COUNTY: W side of Jenny Lake, Grand Teton Mtns. (*U1054*).

Sedum divergens S. Wats. (n = 8.)

Washington. CHELAN COUNTY: 5 mi. W of Merritt, 12 mi. E of Stevens Pass (*U1815*); KITTITAS COUNTY: Keechelus Lake, SE of Snoqualmie Pass (*U1819*); PIERCE COUNTY: White River, 28 mi. E of Enumclaw (*U382*); 0.25 mi. E of Cayuse Pass (*U381*). **Oregon.** HOOD RIVER COUNTY: east side of Mt. Hood (*U1033*). LINN COUNTY: Tombstone Pass, 4200′ (*U1183*).

Sedum lanceolatum Torrey subsp. **lanceolatum** and subsp. **subalpinum** (Blankinship) Clausen. (n = 8.)

British Columbia. 7 mi. S of Merritt, 3500′ (*U1953*); 9 mi. N of Princeton, n = 8 + 1B, 2300′ (*U1954*); 18 mi. E of Princeton, 1200′ (*U1955*); Crowsnest Pass, ¼ mi. W of Alberta border (*U391*). **Alberta.** BANFF NATIONAL PARK: Mt. Whitehorn, E of Lake Louise, 6750′ (*U1811*); Mt. Norquay lift, Banff, 6900′ (*U1810*). WATERTON LAKES NATIONAL PARK: 5 mi. N of Cameron Lake

(*U393*). **Oregon.** JACKSON COUNTY: near summit, Mt. Ashland, Klamath Mtns., 7200′ (*U1971*). **California.** SISKIYOU COUNTY: Scott Mt., 5700′ (*U1977*). **Montana.** FLATHEAD COUNTY: 2 mi. NW of Logan Pass (*U400*); 1.8 mi. W of Marias Pass (*U1806*). GLACIER COUNTY: Rising Sun, Glacier National Park (*U398, U1198*); 3 mi. SW of East Glacier (*U1804*). TETON COUNTY: N Fork, Teton River, W of Choteau, 6000′ (*M. Williams*) (*U1567*). CASCADE COUNTY: Little Belt Mtns., 2.5 mi. S of Neihart (*U1803*). BROADWATER COUNTY: 22 mi. E of Townsend, Big Belt Mtns. (*U1801*). GALLATIN COUNTY: Gallatin River, 27 mi. S of Bozeman (*U1049*). **Wyoming.** YELLOWSTONE NATIONAL PARK: 9.7 mi. W of Tower Junction (*U1794*); 1.6 mi. SE of Tower Junction (*U2172*); decomposing geyserite near Giantess Geyser, 350 meters N of Old Faithful (*U1052*). WASHAKIE COUNTY: 16 mi. NE of Tensleep, Big Horn Range (*U1774*). NATRONA COUNTY: Hells Half Acre, 4 mi. W of Powder River (*U1195*). ALBANY COUNTY: Vedauwoo Glen, 18 mi. SE of Laramie, Sherman Mtns. (*U1075, U1735*); Tree-in-Rock, 20 mi. SE of Laramie (*U1998*). LARAMIE COUNTY: 22 mi. W of Cheyenne, Sherman Mtns. (*U1736*). **Utah.** SUMMIT COUNTY: 6 mi. N of Mirror Lake, Uinta Mtns. (*U1988*); Bald Mountain Pass, 29 mi. E of Kamas, 10650′ (*U1986*); 22 mi. E of Kamas (*U1985*). DUCHESNE COUNTY: Mirror Lake, Uinta Mtns., 9950′ (*U1987*). **Colorado.** LARIMER COUNTY: 4.5 mi. NW Virginia Dale, Sherman Mtns., 7700′ (*U2196*); Rawah Wild Area, 10,800′ (*D. D. Koob*) (*U532, U687*); Alpine tundra, Fall River Pass, 11,800′ (*U1067*); Fall River Road, 10,000′ (*U2208A*, $n = 9 + 1$; *U2208B, U2208C*, $n = 8$); Trail Ridge, 4.4 & 6.7 mi. SE of Fall River Pass, 12,125 & 11,800′ (*U2210, U2211*); Horseshoe Park, (*U2207*); 4.5 mi. W of Estes Park (*U2212*); W side of Estes Park (*U1070*); E side of Estes Park (*U2206*); 5 mi. S of Estes Park (*U2205*); 6 mi. SE of Estes Park (*U2213*); 2.7 mi. N of Meeker Park (*U2204*); Big Thompson Canyon, 15 mi. W of Loveland (*U1071*); 1.5 mi. NW Pinewood Springs (*U2214*). GRAND COUNTY: 6.3 mi. SW Milner Pass (*U1065**). BOULDER COUNTY: 5 mi. SE Pinewood Springs (*U2215*); 2.5 mi. S of Meeker Park (*U2203*); 2.5 mi. NW of Raymond, 9000′ (*U2202*); 6 mi. N of Ward, 9300′ (*U2201*); 0.5 mi. N of Ward (*U2200*); 7 mi. N of Nederland, 8600′ (*U2199*); 4 mi. W of Boulder (*U2197*); Chautauqua, Boulder (*U1340*); Eldorado Springs (*U1339*). CLEAR CREEK COUNTY: Idaho Springs, 7700′ (*U2228*); 5 mi. SW of Idaho Springs (*U1334*). JEFFERSON COUNTY: 13 mi. W of Denver, 7500′ (*U2232*); Bergen Park (*NY Bot. Gard.*) (*C46–39*); 3 mi. SW Morrison (*U1588*); 1 mi. SW Conifer Junction (*U1589*); 1 mi. NE of Silver Springs (*U1590*); 1.6 mi. S of Buffalo Creek (*C. H. Uhl, Jr.*) (*U2279*). PARK COUNTY: Kenosha Pass, 10,000′ (*U1591*). GUNNISON COUNTY: 7.5 mi. NE of Almont, 8600′ (*U2241*). CUSTER COUNTY: Wet Mtns., 9 mi. NW of Fairview (*U1603*); Fairview, 9300′ (*U1602*); 5.5 mi. NW San Isabel (*U1601*); San Isabel, $n = 8 + 1$ (*U1600*). PUEBLO COUNTY: 4 mi. NW Rye (*U1599*). MINERAL COUNTY: 4.5 mi. W of Wolf Creek Pass, San Juan Mtns. (*U1595*). HUERFANO COUNTY: 1.5 mi. E of La Veta Pass, Culebra Range, 9200′ (*U1596*).

Sedum lanceolatum Torrey subsp. **lanceolatum** and subsp. **subalpinum** (Blankinship) Clausen. ($n = 16$.)

Washington. PIERCE COUNTY: Castle Mt., NE of Mt. Rainier, 6500′ (*M. Williams*) (*U1254*). **Oregon.** GRANT COUNTY: serpentine 1 mi. E of Dixie Pass, Blue Mtns. (*U1190*). WALLOWA COUNTY: N slope, Joseph Mt., Wallowa Mtns., 7000′ (*M. Williams*) (*U1562*). **Nevada.** ELKO COUNTY: near Angel Lake, East Humboldt Range (*M. Williams*) (*U1223*). **Montana.** MEAGHER-CASCADE COUNTY LINE: Kings Hill Pass, Little Belt Mtns., 7400′ (*U1802*). PARK COUNTY: 0.4 mi. W of Silvergate (*U1791*); Colter Pass, 8060′ (*U1790*). CARBON COUNTY: Rock Creek Observation Point, 21 mi. SW Red Lodge (*U1785**); 13 mi. SW of Red Lodge (*U1784*); 4 mi. SW of Red Lodge (*U1783*). **Wyoming.** YELLOWSTONE NATIONAL PARK: 8 mi. E of Tower Junction (*U1793*); 20 mi. E of Tower Junction (*U1792*); 22 mi. E of Tower Junction (*U2171*); below Virginia Cascades (*U1800*); spur road to Mt. Washburn, 8200′ (*U1051**); Canyon Junction (*U2184*); Hayden Valley, 9 mi. S of Canyon Junction (*U2187*); 1 mi. N of Lake Junction (*U2188*); spur road to Natural Bridge (*U403*); 4.25 mi. SW of Lake Junction (*U2189*); 10 mi. NE West Thumb (*U2190*); 3.2 mi. NW of West Thumb, 8300′ (*U2191*). PARK COUNTY: Clarks Fork, 9.75 mi. SE of Cooke City, Mont. (*U1789**); 1 mi. W of Beartooth Lake (*U1788**); alpine tundra at Beartooth Pass, 10,950′ (*U1787*); 3.5 mi. N of Beartooth Pass, in alpine tundra (*U1786*). BIG HORN COUNTY: W side Medicine Mt., Big Horn Range, 29 mi. E of Lovell (*U1782**); near Bald Mt. Campground, 37 mi. E of Lovell (*U1780*); 15 mi. W of Burgess Junction, Big Horn Range (*U1779**); 3.75 mi. above Shell Falls (*U1775*); 1 mi. above Shell Falls (*U405*). SHERIDAN COUNTY: N Tongue River, 10 mi. W of Burgess Junction (*U1778*); 0.25 mi. W of Burgess Junction (*U2170*); 0.5 mi. N of Granite Pass, 8900′ (*U1776*); 7.75 mi. E of Burgess Junction (*U2169*); 13 mi. W of Dayton (*U2168*). WASHAKIE COUNTY: Meadowlark Lake, Big Horn Range (*U1773*). JOHNSON COUNTY: alpine tundra at Powder River Pass, Big Horn Range, 9670′ (*U1772*); 3 mi. E of Powder River Pass (*U1771*); 25 mi. SW of Buffalo (*U1770*); 16 mi. W of Buffalo, Big Horn Range (*U1768*). CARBON COUNTY: Arlington, in gravelly roadside (*U1995*); 6.75 mi. N of Riverside (*U1727*); 16.5 mi. SE of Saratoga (*U1728*); above Silver Lake, Snowy Range (*U1729*); Libby Flats, Snowy Range, 10,800′ (*U1730*). ALBANY COUNTY: 1.25 mi. W of Centennial (*U1732*); 12 mi. SE of Laramie (*U1996*); 6 mi. E of Laramie, Sherman Mtns. (*U1733*); 9.5 mi. E of Laramie (*U1734*); 2 mi. SE of Tie Siding (*U2194*); 4.25 mi. SE of Tie Siding (*U2195*). **South Dakota.** PENNINGTON COUNTY: 1.5 mi. W of Mt. Rushmore (*U1764*). CUSTER COUNTY: S of Hood Tunnel (*U1765*); Needles Eye (*U1766*); 0.5 mi. E of Stockade Lake (*U1767*). **Utah.** SAN JUAN COUNTY: Pine Ridge, 3.7 mi. E of La Sal, La Sal Mtns. (*U1614*). **Arizona.** APACHE COUNTY: Tsaile Creek, 15.6 mi. N of Wheatfield Lake on Roof Butte Road, Chuska Mtns., 8000′ (*C. H. Uhl, Jr.*) (*U2285*). **Colorado.** GRAND COUNTY: Hot Sulphur Springs (*U1064*); 9.5 mi. NW of Granby (*U1722*); Milner Pass, 10,760′ (*U1066*); Big Meadows, 4 mi. N of Grand Lake (*U2227*); Cascade Falls, 4 mi. NE of Grand Lake (*U2226*); E side Grand Lake, 8400′ (*U2220*); N tip, Granby Lake (*U2221*); SW corner, Granby Lake (*U2222*); S side Granby Lake (*U2224*); 0.5 mi. W of Monarch Lake (*U2223*); 1 mi. N of Granby (*U1720**); 0.5 mi. N of Fraser (*U1719*); 3.5 mi. N of Berthoud Pass (*U1717*); Berthoud Pass, 11,320′ (*U1716*). CLEAR CREEK COUNTY: 7.5 mi. W of Empire (*U1715*); 4.25 mi. W of Empire (*U1714*); Loveland Pass, in tundra, 12,000′ (*U1333*); W side of Dillon Reser-

voir, 2 mi. N of Frisco (*U1713*); 1.75 mi. S of Frisco, 9300′ (*U2233*); 5.75 mi. SE of Frisco (*U2234*); 1.75 mi. SE of Vail Pass, 10,300′ (*U2276*); 1 mi. N of Climax, 11,250′ (*U1330*). PITKIN COUNTY: 10 mi. W of Independence Pass, Sawatch Range (*U1611*). EAGLE COUNTY: Tennessee Pass, 10 mi. N of Leadville, 10,425′ (*U1707*). LAKE COUNTY: 7.5 mi. N of Leadville (*U1706*); 5 mi. SW of Climax (*U1705*); 13 mi. W of Twin Lakes, Sawatch Range (*U1606*); 7 mi. W of Twin Lakes, 10,000′ (*U1605*); 1.5 mi. W of Twin Lakes (*U1604*). PARK COUNTY: 2 mi. S of Alma (*U2236*). MONTROSE COUNTY: Campground and Oragon Point, Black Canyon of the Gunnison National Monument (*U1697, U2284*). GUNNISON COUNTY: S side of Taylor Reservoir (*U2240*); 8 mi. W of Cottonwood Pass, Sawatch Range, 10,400′ (*U2239*); Monarch Pass, 11,350′ (*U1328*). CHAFFEE COUNTY: 4 mi. N of Monarch Pass, 10,000′ (*C. H. Uhl, Jr.*) (*U2282*). TELLER COUNTY: Middle Beaver Creek, 0.5 & 3.3 mi. N of Clyde Campground, 7 & 4.5 mi. S of Pikes Peak summit, 9550′ & 10,900′ (*C. H. Uhl, Jr.*) (*U2281, U2280*). SAN MIGUEL COUNTY: 4.25 mi. N of Lizard Head Pass, La Plata Mtns., 0.5 mi. S of Ophir (*U1696*). OURAY COUNTY: Ouray (*U1325*); 1.5 mi. S of Ouray (*U1324*). SAN JUAN COUNTY: Red Mountain Pass, 11,090′ (*U1322*); 16 mi. S of Silverton (*U1318*). HINSDALE COUNTY: 2 mi. S of Lake City (*U1694*). MINERAL COUNTY: North Creede, 9100′ (*U1592*); 7 mi. NE of Wolf Creek Pass (*U1594*). HUERFANO COUNTY: Blue Lakes, above Cucharas Pass, Culebra Range, 10,000′ (*U1597*). **New Mexico.** TAOS COUNTY: 2.7 mi. E of Questa (*U1139*). COLFAX COUNTY: 2.5 mi. E of Red River Pass, Sangre de Cristo Range (*U1135*).

Sedum lanceolatum Torrey subsp. **lanceolatum.** (*n* = 24.)

British Columbia. W end of Yellow Lake, 17 mi. SW Penticton (*U1813*). **Washington.** CLALLAM COUNTY: Olympic Mtns. (*W. C. Muenscher 813*). OKANOGAN COUNTY: near dam, Conconully Lake (*U1957*). CHELAN COUNTY: Mission Ridge Ski Area, 11 mi. SE of Wenatchee (*U1814*). **Idaho.** BONNER COUNTY: Cabinet Gorge Dam (*H. W. Blaser*) (*U1817*). BONNEVILLE COUNTY: 10 mi. N of Swan Valley, Big Hole Mtns. (*U1192*). **California.** ALPINE COUNTY: Carson Pass, 8600′ (*U1163*); above Blue Lakes, S of Carson Pass (*P. C. Hutchison 2149*) (*U985*). MONO COUNTY: 1 mi.N of Tioga Pass (*U974*). **Nevada.** HUMBOLDT COUNTY: E slope, Granite Peak, Santa Rosa Mtns., 8500′ (*R. Ornduff*) (*U1010*). ELKO COUNTY: along Jarbridge River, Jarbridge Mtns. (*M. Williams*) (*U1225*). LANDER COUNTY: S of Austin Summit, Toiyabe Mtns. (*U1117, U1161*). NYE COUNTY: above Cherry Creek Summit, Quinn Canyon Range (*M. Williams*) (*U1362*). **Utah.** KANE COUNTY: 0.5 mi. N of E entrance, Zion National Park (*U1160*). **Montana.** GALLATIN COUNTY: West Yellowstone (*U2177*). **Wyoming.** YELLOWSTONE NATIONAL PARK: 4 mi. E of West Entrance (*U2176*); 5.75 mi. W of Madison Junction (*U2175*); 2.25 mi. W of Madison Junction (*U2178*); rotting travertine at Mammoth Hot Springs (*U1050*); 10 mi. S of Mammoth Hot Springs (*U2183*); 6.5 mi. N of Norris Junction at Beaver Ponds (*U2182*); 0.75 mi. W of Gibbon Falls (*U2181*); 2 mi. E of Madison Junction (*A. Witztum*) (*U1196*); Firehole Canyon (*U2179*); S side, Firehole Lake (*U1795*); 1.4 mi. S of Firehole Lake (*U2173*); observation point, Old

Faithful (*U1796**). PARK COUNTY: Pahaska (*J. M Kingsbury*) (*U432*). TETON COUNTY: W side of Jenny Lake (*U1053*); 2 mi. S of Jenny Lake, in sagebrush (*U2192*); 1.5 mi. W of Togwotee Pass, Wind River Range, 9300′ (*U1194*). LINCOLN COUNTY: 7.5 mi. NE of Alpine (*U1055*). **Colorado.** EAGLE COUNTY: 8 mi. S of Gilman (*U1708*); 8.7 mi. SE of Vail, 9200′ (*U2217*). SUMMIT COUNTY: 2.25 mi. SE of Vail Pass, Gore Range (*U1710, U2216*); 4.75 mi. SE of Vail Pass, 9900′ (*U1711*); 5.5 mi. SW of Frisco (*U1331*); 4.75 mi. SW of Frisco (*U1712*).

Sedum lanceolatum Torrey subsp. **nesioticum** (G. N. Jones) Clausen. (*n* = 24.)
British Columbia. Cattle Point, Victoria (*U385*). **Washington.** WHATCOM COUNTY: Lummi I. (*W. C. Muenscher 7931*).

Sedum leibergii Britton. (*n* = 8.)
Oregon. HOOD RIVER COUNTY: 1 mi. E of Hood River (*U1035*). WASCO COUNTY: 2.5 mi. W of Celilo (*U1037*); Cow Canyon, 2.5 mi. N of Willowdale (*U1961*). WHEELER COUNTY: Mitchell (*U1185*); Mountain Creek, 17.5 mi. E of Mitchell (*U1186*); 20 mi. E of Mitchell, 3450′ (*U1187*). GRANT COUNTY: Rock Creek, 7.75 mi. W of Dayville (*U1188**).

Sedum oreganum Nuttall subsp. **oreganum.** (*n* = 12.)
British Columbia. Horseshoe Bay, 20 mi. N of Vancouver (*UC62.306*). **Washington.** WHATCOM COUNTY: Lummi I. (*W. C. Muenscher 7923*); Ruby Creek (*W. C. Muenscher 7929*). PACIFIC COUNTY: N side of Cape Disappointment, S of Ilwaco (*U1027*). WAHKIAKUM COUNTY: 4 mi. E of Cathlamet (*U1029*). **Oregon.** TILLAMOOK COUNTY: sea bluff, 4 mi. N of Nehalem (*U379*). LANE COUNTY: sea cliffs, 6 mi. S of Yachats (*U378*).

Sedum oreganum Nuttall subsp. **tenue** Clausen. (*n* = 12.)
Washington. PIERCE COUNTY: White River, 28 mi. E of Enumclaw (*U383*); SW entrance to Mt. Rainier National Park (*U1178*). KITTITAS COUNTY: Keechelus Lake, 7 mi. E of Snoqualmie Pass (*U1818*). LEWIS COUNTY: Cowlitz River at Nesika (*U380*). **Oregon.** MULTNOMAH COUNTY: Sandy River, 2 mi. S of Troutdale (*R. Bacigalupi et al.*) (*U978*); Latourelle Falls (*R. Bacigalupi et al.*) (*U980*); Sheppards Dell (*R. Bacigalupi et al.*) (*U982*). LINN COUNTY: Tombstone Pass, 4200′ (*U1181*).

Sedum radiatum S. Wats. subsp. **radiatum.** (*n* = 8.)
California. HUMBOLDT COUNTY: Klamath River, 4 mi. N of Orleans (*U936*). MENDOCINO COUNTY: 3 mi. SE of Cummings (*M. Kimnach 56*) (*U371*); 5.25 mi. SE of Cummings (*U929*); 3 mi. S of Longvale (*M. Kimnach*) (*UC53.493*). LAKE COUNTY: 6 mi. SE of Lakeport (*R. Moran 3385*). SONOMA COUNTY: N of Occidental (*H. Roberts*) (*UC52.496*). NAPA COUNTY: 6 mi. NE of Calistoga (*M. A. Nobs*) (*M3245*). MARIN COUNTY: Walker Creek Bridge, 1.5 mi. S of Tomales (*W. Roderick*) (*U1167*); Nicasio Creek, 3 mi. E of Pt. Reyes Station (*U365*); 1 mi. W of Lagunitas, 200′ (*U364*); Upper Lucas Valley, 5 mi. SE of Nicasio (*U362*). SANTA CRUZ COUNTY: 3.5 mi. NW of Boulder Creek (*U924*). SAN BENITO-MONTEREY COUNTY LINE: (TOPOTYPE), near summit of Fremont Peak, 3050′ (*U903*). TUOLUMNE COUNTY: S Fork, Tuolumne River at Cliff

House (*U366*). MARIPOSA COUNTY: Pohono Trail, above Wawona Tunnel, Yosemite National Park (*U367*). FRESNO COUNTY: Stevenson Creek, below Shaver Lake Dam, 5300′ (*U909*).

Sedum radiatum S. Wats. subsp. **depauperatum** Clausen. (*n* = 8.)

Oregon. JACKSON COUNTY: on serpentine (?) along Applegate River, 0.25 mi. S of Copper, 1750′ (*U1968*); 10 mi. SE McKee Bridge (*P. C. Hutchison 962* = *UC62.1115*). **California.** SISKIYOU COUNTY: on serpentine (?), Copper Butte, N of Seiad Valley, 5200′ (*M. Williams*) (*U1213*).

Sedum radiatum S. Wats. subsp. **ciliosum** (Howell) Clausen. (*n* = 8.)

Oregon. JOSEPHINE COUNTY: Grave Creek Bridge over Rogue River (*U950*); Rogue River at Hellgate Bridge, 6 mi. S of Galice (*U947*). DOUGLAS COUNTY: 6.5 mi. S of Tiller (*P. C. Hutchison 2616*) (*UC62.1123*). JACKSON COUNTY: Rogue River at Shady Cove (*U944*); W of McLeod (*U1023*).

Sedum rupicolum G. N. Jones. (*n* = 16.)

Washington. CHELAN COUNTY: (TOPOTYPE), on serpentine along Peshastin Creek, 6.6 mi. N of Swauk Pass, Wenatchee Mtns. (*U1040**). **Cultivated.** Possibly from type clone (see Clausen, 1975) (*C388*).

Sedum stenopetalum Pursh subsp. **stenopetalum.** (*n* = 32.)

British Columbia. W end of Yellow Lake, 17 mi. SW of Penticton (*U1812*). **Alberta.** WATERTON LAKES NATIONAL PARK: 5 mi. N of Cameron Lake (*U394*); Cameron Falls (*U392*). **Washington.** WHATCOM COUNTY: Harts Pass (*W. C. Muenscher*) (*C131*). OKANOGAN COUNTY: 3 mi. NW of Conconully (*U1956*); 1 mi. SE of Desautel Pass (*U390*). KITTITAS COUNTY: Swauk Creek, 9 mi. NE of Teanaway, Wenatchee Mtns. (*U1039*). PEND OREILLE COUNTY: 16 mi. SW of Newport (*U1043*). **Oregon.** COLUMBIA COUNTY: 1 mi. N of St. Helens (*M. Kimnach*) (*UC52.1294*). CROOK COUNTY: Marks Creek, 22 mi. E of Prineville (*U1184*). WHEELER COUNTY: 1.75 mi. E of Ochoco Pass (*J. Weiler et al.*) (*U983*). GRANT COUNTY: 5 mi. S of Long Creek, 4000′ (*M. Williams*) (*U1252*); 1 mi. E of Dixie Pass, Blue Mtns., 5100′ (*U1189*). BAKER COUNTY: 1 mi. E of Blue Mountain Pass (*U1191*). WALLOWA COUNTY: N slope, Joseph Mt., Wallowa Mtns. (*M. Williams*) (*U1565*). **California.** MODOC COUNTY: Cedar Pass, Warner Mtns., 6200′ (*W. Roderick*) (*U966*); 2 mi. NE of Cedar Pass (*M. Williams*) (*U1119*). **Idaho.** BOUNDARY COUNTY: below Moyie Falls, 9 mi. E of Bonners Ferry (*U1045*). BONNER COUNTY: 2.25 mi. W of Laclede (*U1044*). KOOTENAI COUNTY: N shore Lake Coeur d'Alene (*U1820*); East Point, Lake Coeur d'Alene, near Harrison (*G. Bowne*) (*U409*). **Montana.** LINCOLN COUNTY: Kootenai River, 5 mi. SE of Troy (*U1046*); 3 mi. N of Olney (*U1809*). FLATHEAD COUNTY: McGregor Lake, 31 mi. W of Kalispell (*U1047*); Somers (*U1048*); Flathead River, 0.5 mi. E of West Glacier (*U1808*); 16 mi. SE of West Glacier (*U1807*). GLACIER NATIONAL PARK: Many Glacier (*U396*); Rising Sun (*U399, U1197*). MISSOULA COUNTY: Marshall Creek, 4.5 mi. NE of Missoula (*U401*); Clark Fork, 22 mi. SE of Missoula (*U1821*).

Sedum stenopetalum Pursh subsp. **monanthum** (Suksdorf) Clausen. (n = 32.)

Washington. CHELAN COUNTY: Peshastin Creek, 6.5 mi. N of Swauk Pass (*U1041*, mostly one-flowered). **Oregon.** HOOD RIVER COUNTY: near Bottle Prairie, E of Mt. Hood (*U1031*). JACKSON COUNTY: 1 mi. S of Siskiyou Summit (*U942*). **California.** SISKIYOU COUNTY: Copper Butte, N of Seiad Valley, 5200′ (*M. Williams*) (*U1212*). GLENN COUNTY: 6.5 mi. S of Mendocino Pass, 6400′ (*M. Williams*) (*U1248*).

CYTOGEOGRAPHY OF PHACELIA RANUNCULACEA (HYDROPHYLLACEAE)

TSAN IANG CHUANG AND LINCOLN CONSTANCE

Both the occurrence of a disjunct pattern of distribution and the existence of markedly different cytotypes (or chromosome numbers) in the same species are items of considerable interest. When the two phenomena are combined, as they are in *Phacelia ranunculacea* (Nuttall) Constance, the data are worthy of record.

Phacelia ranunculacea (Plate 1) first entered the literature as *Ellisia ranunculacea,* described in 1837 by Nuttall from material that he obtained "in the shady humid alluvial forests of the Arkansas" (Constance 1940, 1949). Since this material was collected and apparently mixed with plants of *Ellisia microcalyx* Nuttall secured at the same time and place, it is not surprising that Gray confused and combined the two under what was known as *Nemophila microcalyx* (Nuttall) Fisch. & Mey. (= *N. triloba* (Raf.) Thieret (1970) = *N. aphylla* (L.) Brummitt (1972) — a singularly inappropriate epithet!). When Watson described *Phacelia covillei* from the Potomac River near Washington, D. C., in 1890, he had no occasion to identify this with a midwestern plant or to seek an earlier epithet in the synonymy of *Nemophila.* The consanguinity of the two entities was postulated by the junior author in 1940, and he included *Phacelia ranunculacea* in his subsequent revision of *Phacelia* subg. *Cosmanthus* (1949).

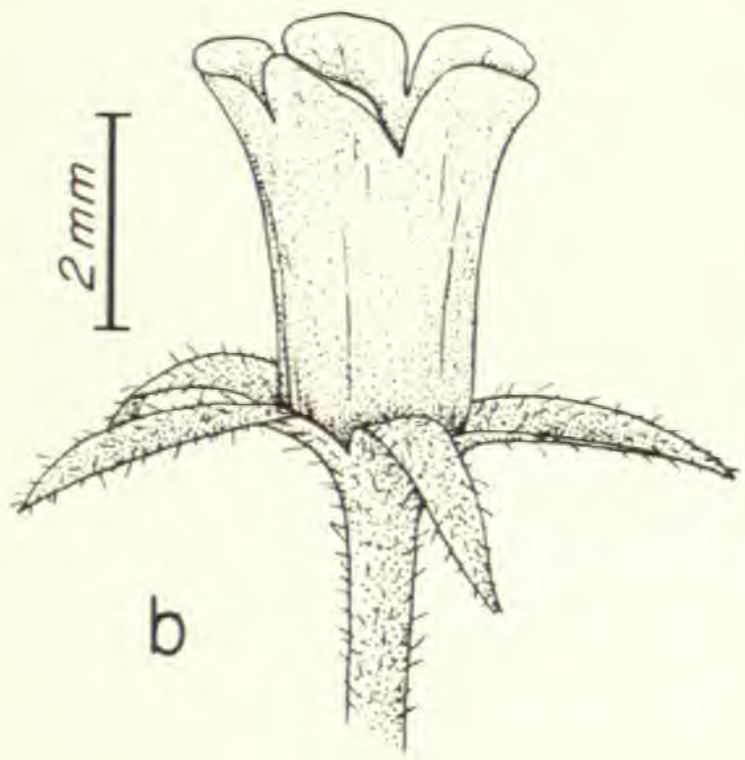
Chromosome numbers for *Phacelia* subg. *Cosmanthus* were ascertained and published some twenty-five years ago (Cave & Constance 1947, 1950; Constance 1949, 1950, 1963) and many of them were confirmed later by Gillett (1964, 1968), by Murdy (1966), and by the senior author (unpublished). Of the eleven species reported, seven had $n = 9$, one had $n = 8$, two had $n = 5$, and *P. ranunculacea* had $n = 14$. Constance remarked with regard to the last: "The arithmetical possibilities of synthesizing *P. ranunculacea,* with 14 pairs, from *P. maculata* or *P. dubia* (both with 5 pairs) and some 9-paired species are very attractive, but it is difficult to see whence one could derive the morphological characteristics that make *P. ranunculacea* so distinctive a plant" (1949, p. 10). Wilson characterized the species as "peculiar in its tubular-campanulate corolla, vestigial glands, semiglobose seeds, chromo-

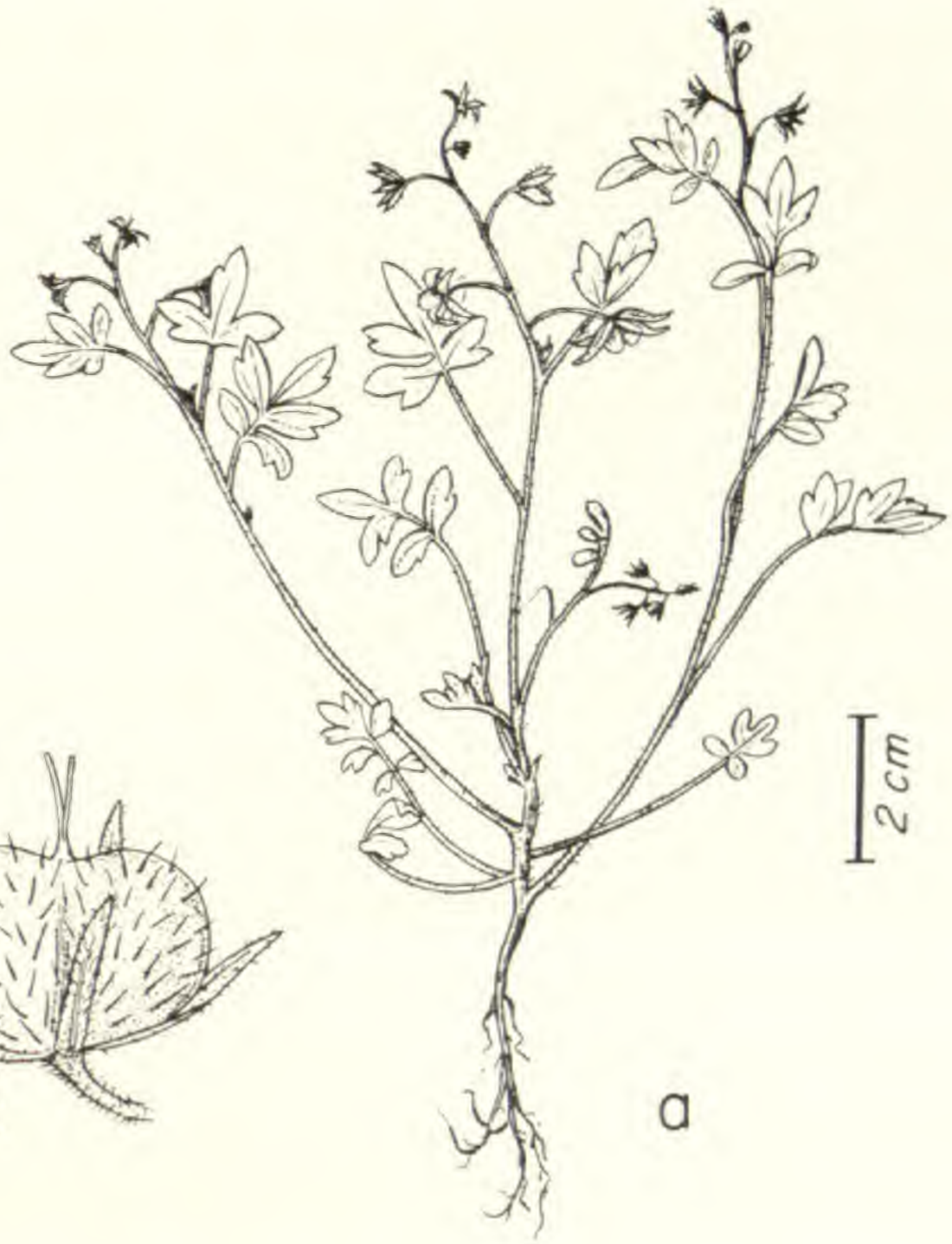
some number, and disrupted distribution . . ." (1960, p. 203). Gillett (1968) placed *P. ranunculacea* in a class (Group I) by itself because of its unequally inserted stamens and unique chromosome number. He also suggested that it is closer to the genus *Nama* than to *Phacelia* and predicted that it "ultimately will be recognized as a monotypic genus" (1968, p. 371).

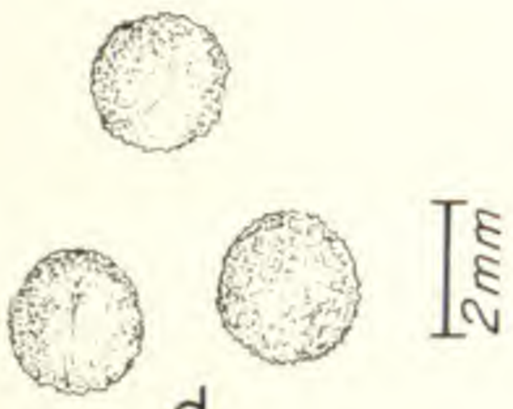
The latter prediction may indeed prove to be true, but the designation of yet another monotypic genus of Hydrophyllaceae — there already are five — does not promise to shed much additional light on relationships. The resemblances to *Ellisia* and *Nemophila* are superficial and depend upon similarity in habit and habitat and in size and shape of corolla. Although the relation of corolla and androecium might suggest *Nama,* the foliage, style and seeds are not compatible with this reference. The genus *Phacelia,* as currently treated, is certainly polymorphic and the placing of emphasis on internal differences could readily lead to generic fragmentation. Conversely, stressing similarities makes it possible to retain this taxon as a large morphologically and cytologically diverse but apparently "natural" grouping, at least until further evidence, perhaps from palynology or biochemistry, leads to a more satisfactory division.

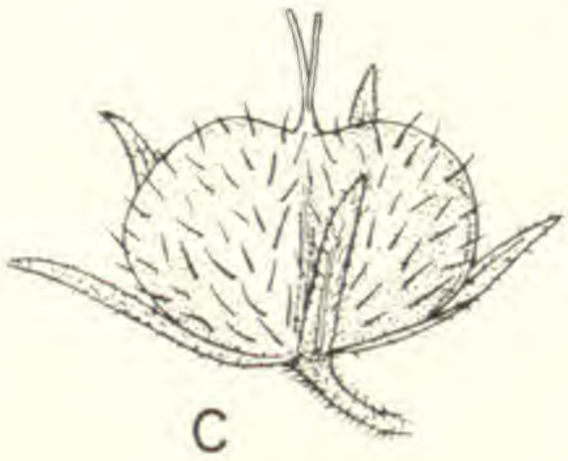
While making a floristic foray into southern Illinois in the spring of 1968, the senior author and his wife obtained vegetative material and buds of plants which appeared referrable to *Phacelia.* When the buds revealed an unexpected chromosome count of $n = 6$, vegetative material was sent to both Gillett and Constance. The latter associated it very tentatively with *P. ranunculacea,* but emphasized the need of flowers and fruit for any positive identification, especially in view of the cytological findings. Complete specimens obtained in Illinois and neighboring states in subsequent years (1969–1973) confirmed the tentative identification. All of these collections proved to have 6 pairs of chromosomes.

These findings raised the possibilities that either there was error in the chromosome number originally reported (which was, after all, based upon a single collection) or that there were undetected morphological differences between the Maryland and the midwestern populations. Successful efforts to obtain East Coast material made it possible to grow the two geographically separated populations together in the greenhouse at Normal,









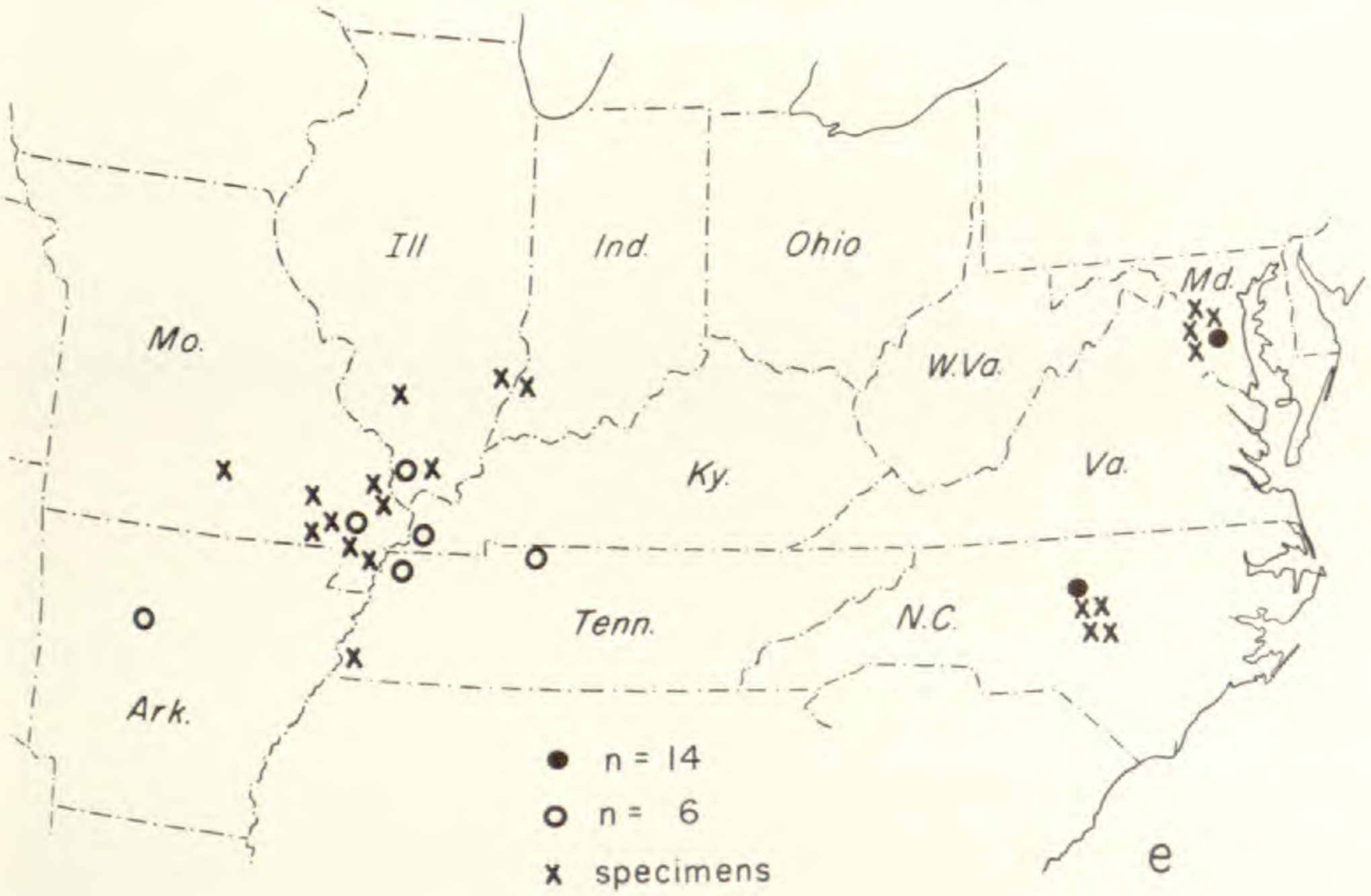


Plate 1. *Phacelia ranunculacea.* a, habit; b, corolla; c, capsule; d, seeds; e, distribution map. (From *Chuang & Chuang 7240, 6851,* and *6856.*)

Illinois, and to confirm the reported chromosome count of $n = 14$ on Maryland and North Carolina plants. The new cytological information may be summarized as follows:

$n = 6$

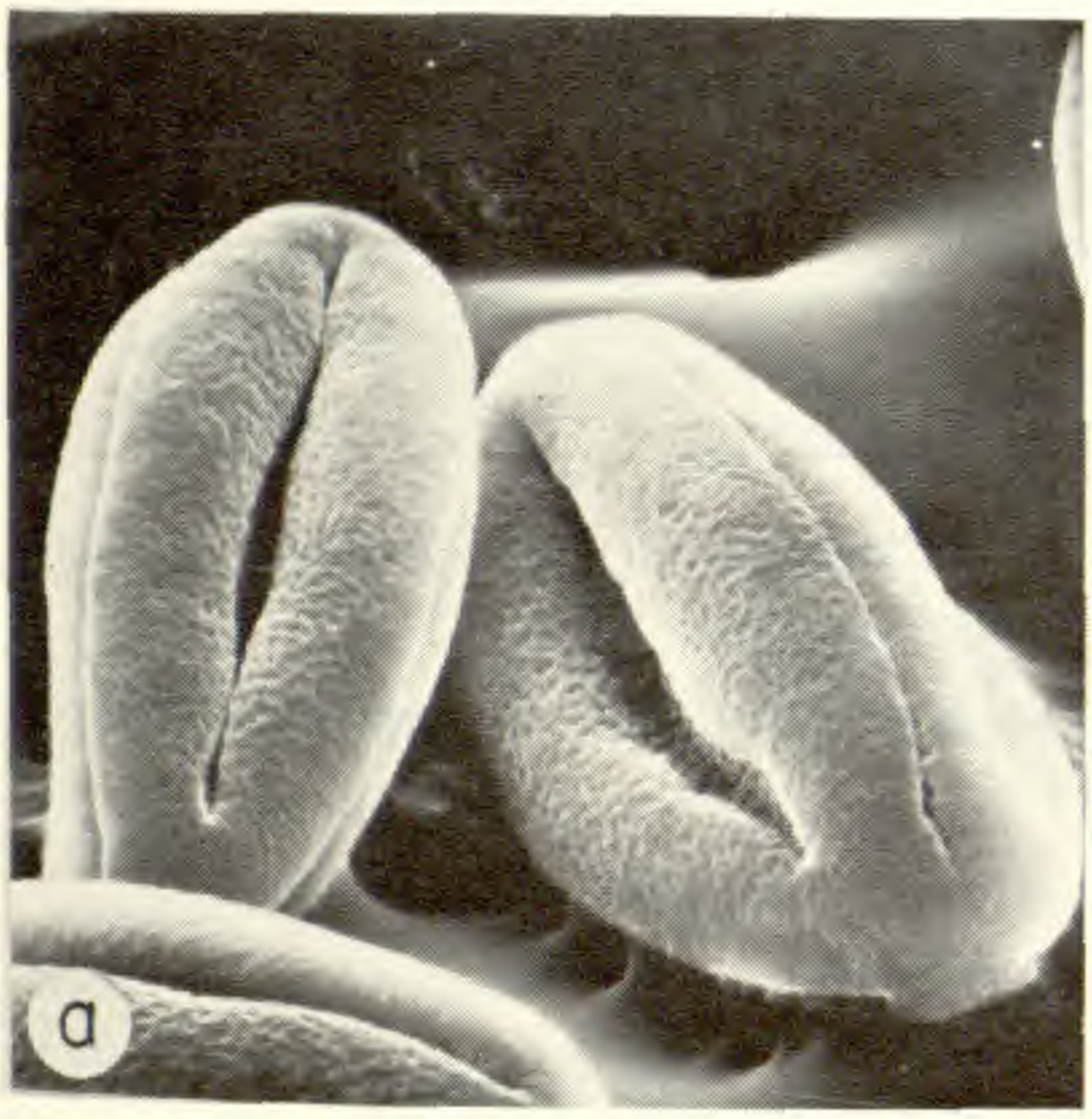
Illinois. UNION CO.: Pine Hill, *Chuang & Chuang 6180, 6608, 6755, 6858, 7240*
Missouri. STODDARD CO.: Agilla, *Chuang & Chuang 6758*
Tennessee. MONTGOMERY CO.: Clarksville, *Chuang & Chuang 6854*
OBION CO.: Walnut Log, *Chuang & Chuang 6855*
Kentucky. HICKMAN CO.: Columbus, *Chuang & Chuang 6856*
Arkansas. POPE CO.: Russellville, *G. Tucker 8478*

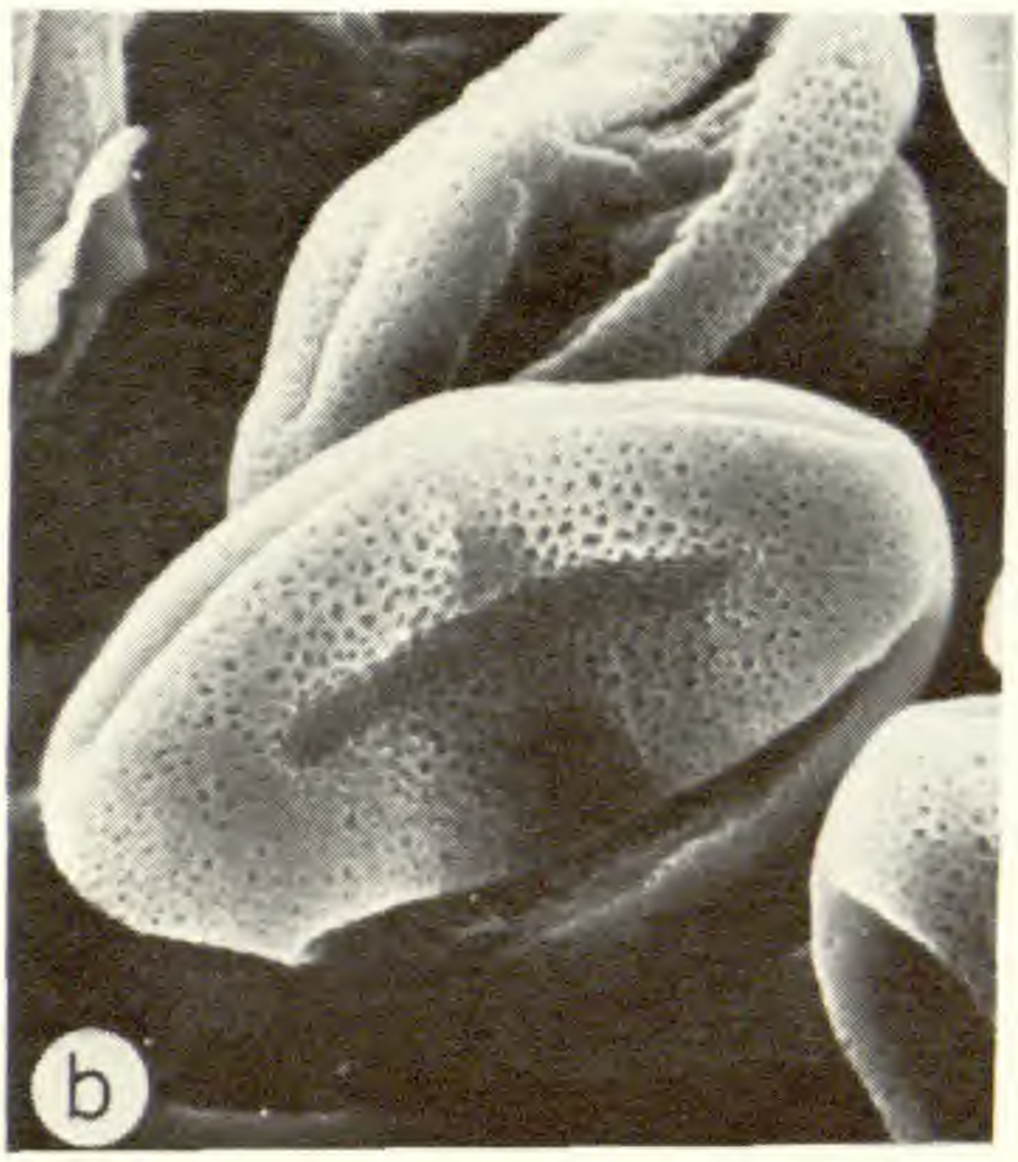
$n = 14$

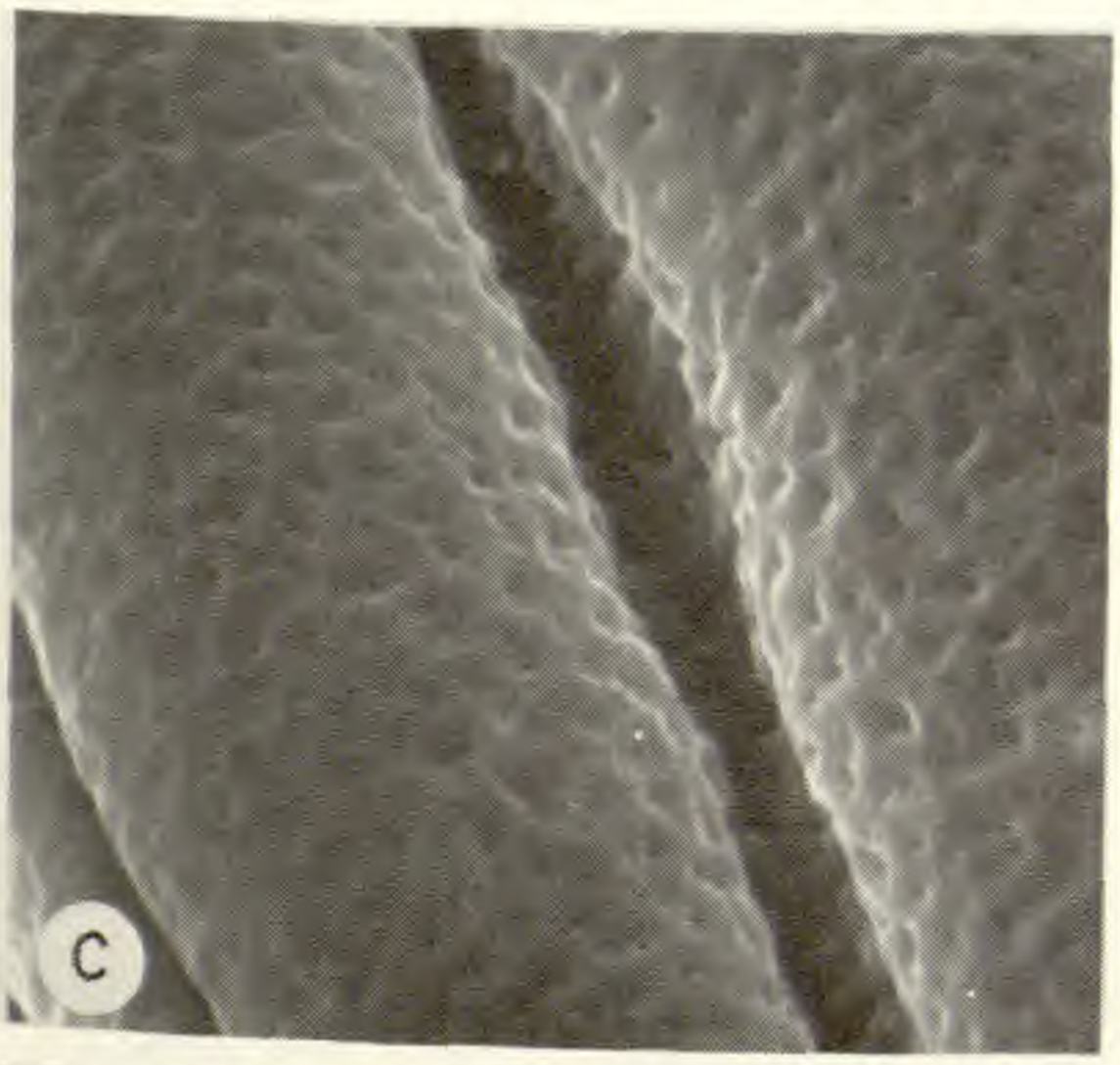
Maryland. MONTGOMERY CO.: Plummers Island, *J. J. Wurdack 2632, Chuang & Chuang 6850*
North Carolina. CHATHAM CO.: Haw River, *Chuang & Chuang 6851*

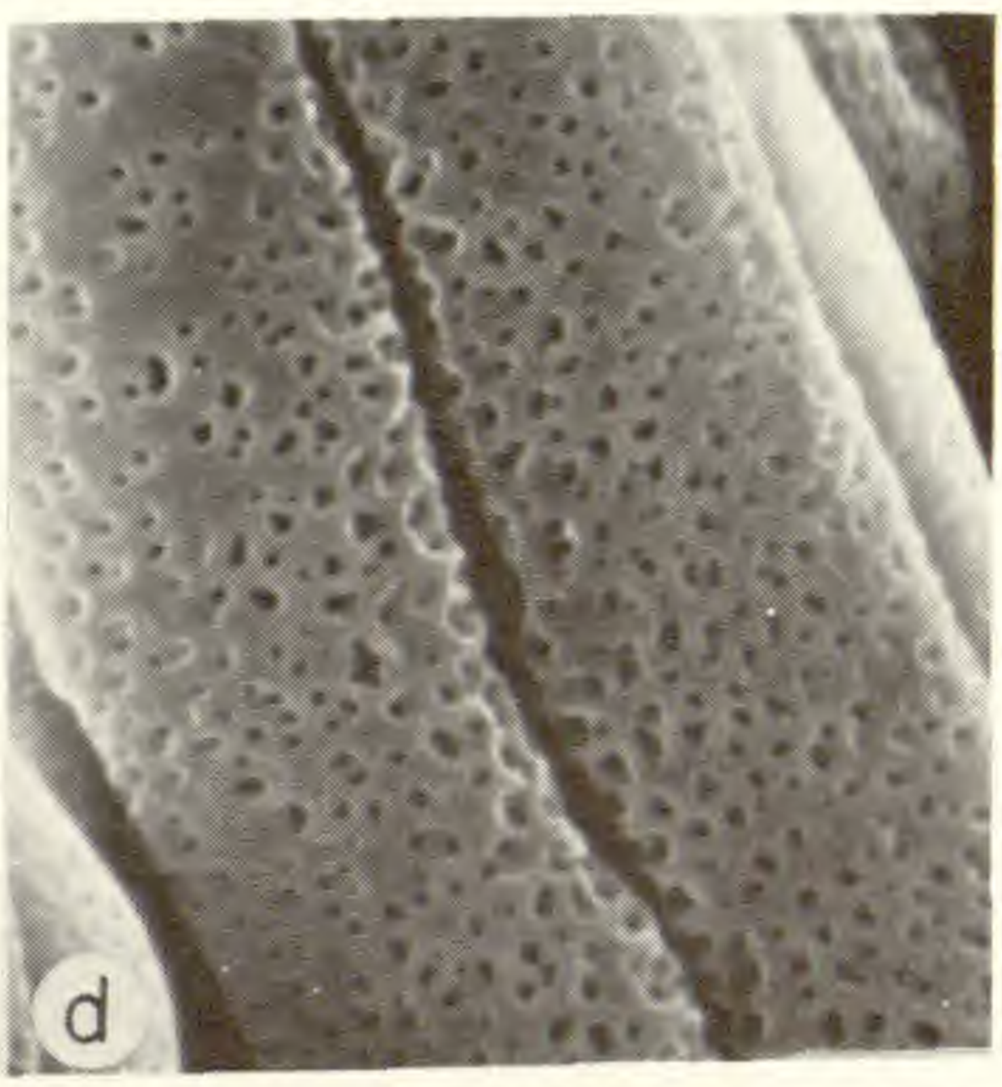
At first it was believed that it might be possible to find at least micro-morphological criteria for separating eastern from mid-western populations, but this prospect diminished with continued investigation in field and in greenhouse. No consistent morphological distinction has been found between the two cytotypes, the pollen and karyotypes of which are shown in Plate 2. The very small size of the tubular-campanulate corollas (exceptional in *Phacelia* and unique in subgenus *Cosmanthus*) and the inclusion of the stamens have unfortunately frustrated all attempts to hybridize members of the two cytotypes.

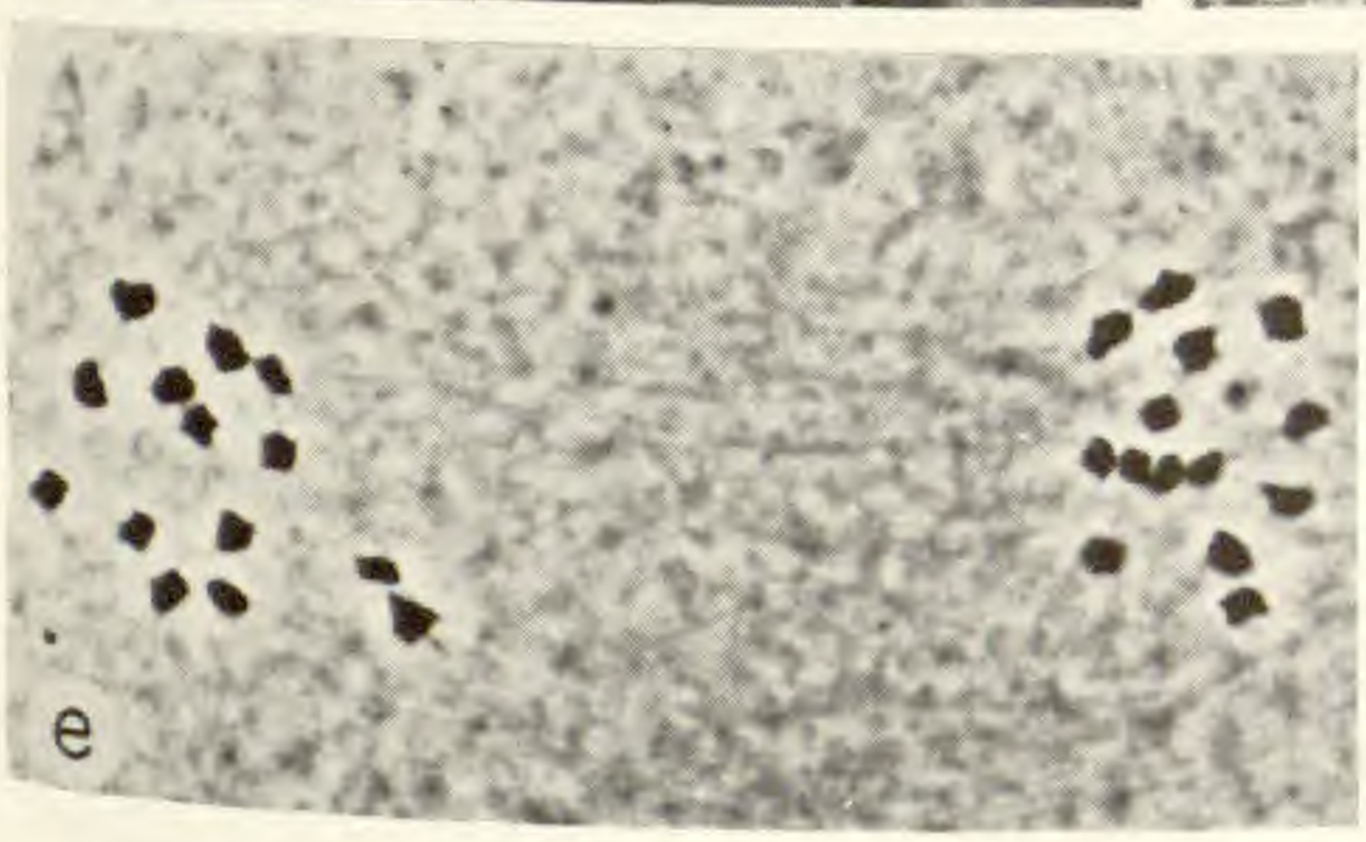
The known distribution of *Phacelia ranunculacea* is shown in the accompanying map (Plate 1e). No exact replica of this pattern has been found. Fernald (1950) suggested that *P. ranunculacea* is "Probably of more general range; easily overlooked or mistaken for *Ellisia nyctelea*" (p. 1194), but this appears to be an inadequate explanation. In his interesting article on Virginia species with disjunct populations in the Midwest, Harvill (1969) lists *P. ranunculacea* as one of only three species primarily of the Atlantic Coastal Plain and restricted in the Midwest to lowland areas. (The other two species are the grass, *Distichlis spicata* (L.) Greene, and the orchid, *Isotria medeoloides* (Pursh) Raf.). He attributes such distributional patterns to migrations in various directions and subsequent contractions of range under changing











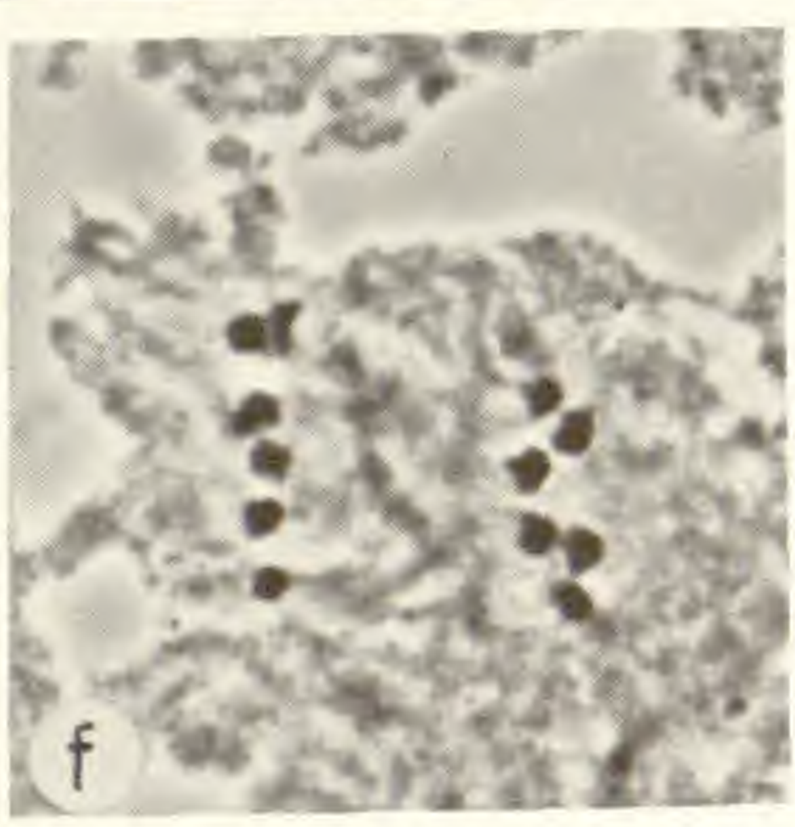


Plate 2. *Phacelia ranunculacea.* Pollen and karyotypes. a, pollen of *6851,* × 1500; b, pollen of *6854,* × 1500; c, pollen surface of *6851,* × 3600; d, pollen surface of *6855,* × 3600; e, karyotype of *6851,* × 880; f, karyotype of *6755,* × 880. (All *Chuang & Chuang* collections, collection data given in the preceding tabulation.)

climatic and physiographic conditions. Such interrupted ranges, he believes, "go far back in geologic time" (p. 229).

Wiggins (1936) indicated that *Iliamna remota* Greene was known from only two stations: an island in the Kankakee River in Illinois, and the summit of Peter's Mountain in Virginia. There is now an additional Virginia station from the James River (Wood, personal communication). The distribution of *Lysimachia radicans* Hook. as mapped by Ray (1956), occurring "in the lower Mississippi River Valley and [with] apparent isolation in Virginia," shows a slight similarity.

Terrell indicates that *Houstonia tenuifolia* Nuttall (= *Hedyotis nuttalliana* Fosberg) possesses an Ozark-Ouachita center and an Appalachian center. "In general, the degree of [morphological] overlap is so great that I have preferred not to distinguish plants of the two centers as separate subspecies, but consider them all part of one variable species. . . . It appears that populations in these two centers have been isolated from each other for a rather long time, long enough for certain differences to arise" (1959, p. 192). Lewis and Terrell (1962) found that populations throughout the range of the species had a chromosome complement of $n = 6$, i.e. diploid.

Carroll Wood has generously called to our attention several other cases of striking disjunction. *Alnus maritima* (Marshall) Nuttall, which may or may not be conspecific with east Asian alders, occurs near the coast of Delaware and Maryland, and then again in southern Oklahoma. Woodson, in his monographic study of the genus *Asclepias* (1954), lists no fewer than eight "bicentric species" of milkweeds, whose occurrence he relates to his Appalachian and Ozarkian centers. The rare *Cotinus obovatus* Raf. is known from Alabama, Tennessee, Arkansas, Oklahoma, and the Edwards Plateau of Texas (Brizicky, 1962). The likewise scarce *Neviusia alabamensis* A. Gray is known from Alabama, Arkansas, and Missouri (Robertson, 1974). None of these, however, offers a strict parallel to the distribution of *Phacelia ranunculacea*.

In *Parthenium hispidum* Raf., Rollins (1950) discovered that var. *hispidum* of the Mississippi Valley appears to be a tetraploid ($2n = 72$), whereas var. *auriculatum* (Britt.) Rollins of the Virginia and North Carolina piedmont appears, on circumstantial evidence, to be diploid ($2n = 36$). If the complements of $n = 6$ and

$n = 14$ can be thought to have any polyploid relationship, then this is the reverse of the *Phacelia ranunculacea* situation, where the inland populations have the smaller chromosome number.

But as Wood (1971, p. 371) thoughtfully reminds us, "a paper like this is not supposed to have definite conclusions, for the basic purpose is to present taxonomic and distributional data . . .", and hopefully some food for thought.

ACKNOWLEDGMENTS

We would like to express our appreciation to all those persons who assisted in the furtherance of this project, but would like particularly to mention the following: R. B. Burton, Jonesboro Ranger Station, U. S. Forest Service, Jonesboro, Ill.; E. W. Chester, Austin Peay State University, Clarksville, Tenn.; John A. Churchill, National Institutes of Health, Bethesda, Md.; Gary Tucker, Arkansas Polytechnic College, Russellville, Ark.; Carroll E. Wood, Jr., Arnold Arboretum and Department of Biology, Harvard University, Cambridge, Mass.; John J. Wurdack, National Museum of Natural History, Smithsonian Institution, Washington, D. C.

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T. I. C.
DEPARTMENT OF BIOLOGICAL SCIENCES
ILLINOIS STATE UNIVERSITY
BLOOMINGTON-NORMAL, ILLINOIS 61761

L. C.
DEPARTMENT OF BOTANY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720

SACCHARUM OR SACCHAROPHORUM ?

ELIZABETH A. SHAW

For years a subject of occasional, but heated, controversy has been the correct name for the common eastern sugar maple. Is it *Acer saccharum* Marshall (1785) or is it *Acer saccharophorum* Koch (1853)? For nearly a century, Marshall's name has been the one more often used, but recently the epithet "saccharophorum" was revived by R. T. Clausen in "Sedum of North America north of the Mexican Plateau" (1975). In discussing the habitat of *Sedum ternatum,* Clausen mentions (p. 106) that in the Ocoee River gorge in southeastern Tennessee this species occurs in the shade of *Acer nigrum* ssp. *saccharophorum* (Koch) Clausen, and in a footnote on this page, the combination actually is made. Unfortunately, the epithet "saccharophorum" cannot be used for the sugar maple, either if it be treated as a species distinct from *A. nigrum* Michx. f., the black maple, or if the two be treated as conspecific.

Linnaeus in Species Plantarum (1753) described nine species of *Acer,* four of them from America; i.e., *A. rubrum, A. saccharinum, A. pensylvanicum,* and *A. Negundo.* He said nothing of the uses or properties of any of these, but his use of the epithet "saccharinum" does suggest that Linnaeus thought that he was describing a species of maple from which sugar is obtained. The specimen which Linnaeus had before him had come from Pehr Kalm who knew the sugar maple well, and had discussed it at length in an article on sugar-producing trees of North America (Kalm, 1751). Post-Linnaean writers on American trees, such as von Wangenheim and the two Michauxes, unhesitatingly accepted the name *Acer saccharinum* for the sugar maple.

In the first volume of Flora of North America, published by Torrey and Gray in October, 1838, the sugar maple appears as *Acer saccharinum* Linn. In November of that year Gray left for Europe with the prime purpose of wresting from European herbaria and botanists ". . . control of the source material on North American plants by resolving disputed points of nomenclature and establishing the Flora as the authoritative base for future work." (Dupree, p. 74. 1959). Toward this end, Gray spent the next year visiting all of the important herbaria in England and

on the continent, and in making detailed notes on the contents of each. In his notes on the Linnaean herbarium one finds under *Acer,* "saccharinum sp. Kalm/only! The spec. is A. eriocarpum!! so is descr." *Acer eriocarpum* is a name for the silver maple, as is *A. dasycarpum* Ehrh. Some of the results of Gray's work in Europe appeared in the supplement (published in June, 1840) to the first volume of the Flora. On page 684 is a short and, to us, startling comment. The specimen from Pehr Kalm in the Linnaean herbarium, the type of the name *Acer saccharinum,* ". . . we find on examination, belongs to A. dasycarpum!" i.e., to the silver maple. Torrey and Gray pointed out that von Wangenheim and the Michauxes had, however, applied the name *Acer saccharinum* to the sugar maple, not to the silver maple, and concluded that ". . . a change in the application of the name would be unwarrantable." As Fernald a century later (1945) pointed out, the days of such enviable innocence are past.

The story behind Linnaeus' confusion has been well described in Rousseau (1940). Kalm had three sets of the collections he made in North America. One, now at LINN, went to Linnaeus, a second set, now at UPS, was given by Kalm to Queen Lovisa Ulrika of Sweden for her herbarium; the third, kept by Kalm, probably was lost in a fire which nearly destroyed the city of Abo̊ (now Turku, Finland) in 1827 (see Juel & Harshberger, 1930). Queen Lovisa Ulrika's specimen of *Acer saccharinum,* so annotated by Kalm himself, is a sugar maple, but Linnaeus received a silver maple.

Although Torrey and Gray were content that the sugar maple remain *Acer saccharinum,* others were not. In his Hortus Dendrologicus (1853) Karl Koch supplied a new name, *A. saccharophorum,* for the sugar maple and there is no doubt that Koch's name refers to this species. Also in his list of maples are *A. nigrum* Michx. f., the black maple, and *A. saccharinum,* under which are several synonyms, among them *A. dasycarpum* Ehrh., all referring to the silver maple. Koch cited "saccharinum Mich. fil hist. d. arbs. for. de l'Amer. sept. . . ." and this is certainly the sugar maple. Michaux has a few lines of diagnostic description, followed by several pages of information on distribution, ecology, characters of the wood, methods of preparing maple sugar, and a recipe for maple beer. *Acer saccharophorum* Koch is a name for the sugar maple.

But is there an earlier name for this species? If one accepts *Acer saccharum* Marshall (1785), there is. Humphrey Marshall of Chester County, Pennsylvania, cousin of John Bartram, was an amateur of botany, and a dealer in seeds and plants, who in 1785 published "Arbustrum Americanum: The American Grove," the first book published in this country on native woody plants. In the introduction Marshall notes that he has used "Linnaean Generic and trivial names (or new formed ones where these have been wanting) together with their most common approved English ones: . . ." There are no synonyms and no references cited, for Marshall felt that most of his readers ". . . would have been more embarrassed and confused than profited thereby . . ." The first genus treated is *Acer,* with six species, including "6. Acer saccharum. The Sugar Maple." Marshall's book was well received in Europe and in 1788 were published, in Paris, a French edition translated and augmented by a M. Lézermes, and in Leipzig, a German edition similarly dealt with by C. F. Hoffmann. Each translator, apparently on his own initiative, changed "saccharum" to "saccharinum." Marshall's *Acer saccharum* was ignored, except when it appeared as a synonym, until 1890 when Britton adopted it for the sugar maple in a list of plants of New Jersey, and it has been generally, although not always, used since then.

The controversy swirls around the epithet "saccharum." Was Marshall's use of this name an error of orthography or typography, or was it the deliberate provision of a name for a species, the sugar maple, at that time not yet described? Marshall did describe several "new species," among them *Betula papyrifera* and *Nyssa sylvatica,* with no indication that they were new. On the other hand, either Marshall or his printer was indeed very careless. Rousseau (p. 40., 1940), strongly anti-"saccharum," provides a list of sixteen, "entres autres" errors of orthography or typography of names in Marshall's book. Even Arbustrum of the title should be "Arbustum."

Rousseau contended that Marshall's name was a simple spelling mistake, and that he included under this name both the sugar and the black maple. In support of the spelling mistake claim, Rousseau cited the name *Acer saccatum* Miller (1771) as an example of another orthographic error and argued that Marshall's name really was no different. But Miller (Gard. Dict. abr. ed. 6.

1771) gave a clear reference to "Lin. Sp. Pl. 1055"; Marshall did not. It is easy to argue that Marshall intended to use the epithet "saccharinum" for the sugar maple, that *Acer saccharum* is a mistake — of no nomenclatural standing, and that the earliest name for the sugar maple is Koch's *A. saccharophorum.* However, one cannot know what Humphrey Marshall intended to do; we know only what he did. He published the name *Acer saccharum.* As for the claim that the name refers both to the sugar and the black maples, many authors, including Torrey and Gray, Rousseau himself, Desmarais (1952), and Clausen, have considered the two to be conspecific; e.g. *Acer saccharophorum* var. *nigrum* (Michx. f.) Rousseau, *A. saccharum* ssp. *nigrum* (Michx. f.) Desmarais, and *A. nigrum* ssp. *saccharophorum* (Koch) Clausen.

Thus *Acer saccharophorum* Koch is not the earliest name for the sugar maple. Moreover, one cannot argue that since a name or an epithet has priority only in its own rank, the epithet "saccharophorum" can, or now must, be used if the sugar maple (in the most narrow sense) is treated as a taxon of infraspecific rank under *A. nigrum* Michx. f. If the sugar and black maples are treated as conspecific, the species must be called *Acer saccharum* Marshall, and the black maple is then, according to one's taste in classification, either *A. saccharum* var. *nigrum* (Michx. f.) Britton, or *A. saccharum* ssp. *nigrum* (Michx. f.) Desmarais.

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GRAY HERBARIUM OF HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MA. 02138

COLOBOGYNE: A TAXONOMIC SYNONYM OF SPILANTHES (COMPOSITAE, HELIANTHEAE)

TOD F. STUESSY

During the preparation of a revised subtribal classification of the tribe Heliantheae of the Compositae (Stuessy, in press), the genus *Colobogyne* Gagnepain was examined to determine its proper subtribal alignment. The present note offers the results of these observations.

Colobogyne was described by Gagnepain (1920) to contain the single species, *C. langbianensis,* from Viet Nam. The closest generic relative of this new taxon was believed to be *Wedelia* Jacq. of the subtribe Helianthinae (= Verbesininae) from which it differed in several distinct features (Gagnepain, 1920). Examination of the holotype of *Colobogyne langbianensis* (*Jacquet 637,* P) indicates clearly that it is a species of *Spilanthes* Jacq. of the subtribe Galinsoginae. Only a few species of *Spilanthes* are known from Asia (Moore, 1907), and one of these, *S. grandiflora* Turcz., is very similar to *Colobogyne* in many features. However, a comparison of an isotype of the former (*Cuming 1154,* MO) with *C. langbianensis* reveals several quantitative differences (e.g., diameter of peduncles and width of outer phyllaries) plus one conspicuous qualitative difference (contrasted respectively): achenes flattened, ciliate at the margins, and with two long awns *vs.* achenes subterete, glabrous, and epappose. In general, the two taxa appear similar enough to be regarded as synonyms except for the achenial characters. Because of this qualitative difference, it seems best to transfer *Colobogyne langbianensis* into *Spilanthes* as a distinct species, pending further intensive studies on the entire genus.

Spilanthes langbianensis (Gagnepain) Stuessy, comb. nov. BASIONYM: *Colobogyne langbianensis* Gagnepain, Not. Syst. (Paris) **4:** 15. 1920.

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DEPARTMENT OF BOTANY
OHIO STATE UNIVERSITY
1735 NEIL AVENUE
COLUMBUS, OHIO 43210

ALLENROLFEA MEXICANA LUNDELL (CHENOPODIACEAE): ITS CONSPECIFICITY WITH A. OCCIDENTALIS (S. WATS.) KUNTZE

ROBERT JANSEN AND BRUCE PARFITT

In a study of some recent collections from Coahuila, Mexico, we were in some doubt as to the identity of certain *Allenrolfea* specimens collected on 27 January 1974 from calcium-baked soil, near the swimming hole (a warm spring) along the highway to Torreón, 9 miles SW of Cuatro Ciénegas (*Jänsen 026, Meyers 004, & Parfitt 564,* all in OSH!). Our specimens are entirely in fruit, and have seeds up to 1 mm long, whereas numerous manual descriptions of *A. occidentalis* (Correll & Correll, 1972; Correll & Johnston, 1970; Davis, 1952; Munz & Keck, 1968; Reed, 1969; Shreve & Wiggins, 1964; Standley, 1922; Wooton & Standley, 1915) allow seed length of only 0.6–0.8 mm. Further, all the works cited above exclude *A. occidentalis* from Coahuila.

Therefore, we investigated the possibility that our plant might be *Allenrolfea mexicana* (Lundell, 1936). Johnston (1944) very amply documented the occurrence of *A. occidentalis* in Coahuila, but his report was apparently overlooked by the post-1944 authors cited above, as it was by Muller (1947) who reported only an "*Allenrolfea* sp." from Coahuila. Lundell says in the protolog, in part, "*Allenrolfea mexicana* differs from *A. occidentalis* (S. Wats.) Kuntze, the Utah form, in being distinctly larger. The woody stem of *A. mexicana* may exceed 2 cm in diameter; the flowering spikes are as much as 6 cm long; and the flowers are regularly 1–3 in the axils of the apical bracts and 3–7 in the axils of the basal bracts. In *A. mexicana* the time of anthesis varies from the apex to the base of the spike, and from the center of the flower aggregate in each axil toward the extremities.

"*Allenrolfea occidentalis* is a smaller form, generally woody only at the base. It has three flowers in the axil of each bract, all of which apparently reach anthesis at about the same time." Lundell further characterizes his species as having "seeds . . . slightly exceeding 1 mm in length" and "branchlets fleshy . . . , internodes 3 to 4 mm thick," and "stigmas . . . each about 1 mm long."

Dr. Rogers McVaugh kindly lent us an isotype of Lundell's plant from a lake at Santo Domingo, San Luis Potosí (*Lundell*

5603, MICH). Examination of the Lundell plant, and comparison with authentic specimens of *A. occidentalis* from Utah (Salt Lake City, Utah. September, 1900. *Cameron Mann 13414.* WIS) and California (San Joaquin County. Shrub 8 feet high, San Joaquin delta, near Holt. 20 September 1928. *Mason 4965.* WIS) revealed that Lundell's plant falls entirely within the range of variation of *A. occidentalis* as that species is generally understood. Mason's plant is up to 8 feet tall, a character which Lundell considered diagnostic for his *A. mexicana;* the degree of woodiness in *A. occidentalis* is highly variable, and the woodiness is not confined to the base, as Lundell and many manuals suggest. Spike length is extremely variable; on the isotype of *A. mexicana,* the longest spike is 2.5 cm long, with many being less than a centimeter long, which falls within the range of *A. occidentalis.* With respect to the pattern of anthesis within the spike and within the axil of each bract, the spikes of, for example, *Mann 13414* appear identical in every respect to those on *Lundell 5603.* Seed length on our Coahuila specimens of *A. occidentalis* varies from 0.8–1.0 mm, and the Mann specimen from Salt Lake City (the type locality) has seeds up to 1 mm long. In *A. mexicana,* the internodes of the branchlets are said by Lundell to be 3–4 mm in width, but the isotype specimen has branchlets only up to 2 mm thick, which demonstrates the degree of variability in this character, even in the type collection. With respect to stigmas, the length of those on the isotype is only 0.5 mm, not 1 mm as Lundell states in the type description; in all specimens of *A. occidentalis* cited here, the stigmas are likewise only 0.5 mm long.

Because we can find no distinguishing characters, we therefore conclude that *Allenrolfea mexicana* Lundell is conspecific with *A. occidentalis.*

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BIOLOGY DEPARTMENT
UNIVERSITY OF WISCONSIN — OSHKOSH
OSHKOSH, WISCONSIN 54901

SUAEDA CALCEOLIFORMIS, THE CORRECT NAME FOR SUAEDA DEPRESSA AUCT.

J. McNeill, I. J. Bassett and C. W. Crompton

Most current taxonomic treatments of the genus *Suaeda* (e.g. Fernald 1950; Gleason & Cronquist 1963; Hitchcock & Cronquist 1964; Hopkins 1975) recognize, under the name *S. depressa,* an annual species occurring on saline and alkaline soil from Alaska and Yukon southward, east of the Cascades, to Minnesota and Texas. On seeking to typify the epithet *depressa,* we found that the name is being misapplied, and that this species should be called *S. calceoliformis* (Hooker) Moquin.

Suaeda depressa (Pursh) S. Watson in King, Rep. U. S. Geol. Explor. Fortieth Parallel **5:** 294. 1871, is based on *Salsola depressa* Pursh, Fl. Amer. Sept. 197. 1814. In publishing *Salsola depressa,* Pursh gives a three-line diagnosis followed by:

> Sueda prostrata. *Pall. illustr.* 55. *t.*47.
> On the volcanic plains of the Missouri. *Nuttall.* ☉.
> June. +.

Because the Pallas synonym was based on plants from southern European Russia and Pursh was writing about the North American flora, attention has concentrated, in applying the epithet *depressa,* on the reference to a Nuttall specimen. Hopkins (1975, p. 27) was unable to locate such a specimen, and Nuttall's name is not included by Watson (1874, p. 89) among the many collectors of specimens of *Suaeda depressa.*

The key to understanding Pursh's use of the name rests on the symbol + at the end of the protologue. To quote the words of the Preface (Pursh, 1814, p. xxi): "Those [i.e., species] I have adopted without seeing them myself in either state [i.e., living or as a dried specimen], and which are but few, I have marked (+)." So Pursh says that he never saw a specimen of his *Salsola depressa* but "adopted" the species from Pallas' description and illustration. This is confirmed by a comparison of Pursh's description with Pallas' account. The former comprises Pallas' diagnosis with the addition of a few words from his description (see Appendix). Pursh included the species in his Flora, only because in some

way he had come to believe that, on the plains of the Missouri, Nuttall had collected a specimen referable to *Suaeda prostrata* Pallas. The complicated histories of Nuttall's 1810–1811 collections (Graustein, 1967) and of Pursh's preparation of his Flora (Ewan, 1952) make this quite plausible.

Salsola depressa Pursh is, therefore, a substitute name for *Suaeda prostrata* Pallas; it is a legitimate substitution because of the existence of *Salsola prostrata* L. (Sp. Pl. 222. 1753), the basionym of *Kochia prostrata* (L.) Schrader. As a substitution, the type of Pursh's epithet *depressa* is the same as that of Pallas' *prostrata.* Accordingly *Suaeda depressa* (Pursh) S. Watson is a homotypic (nomenclatural or obligate) synonym of *Suaeda prostrata* Pallas. This name applies to Eurasian plants which either represent a saline steppe species closely related to *S. maritima* (L.) Dumort. (Il'in, 1936), or else are included within *S. maritima* subsp. *maritima* (Ball, 1964). Whichever treatment is followed, there is no doubt that the Eurasian plants are not conspecific with the American ones to which the name *S. depressa* has hitherto been applied.

Among earlier botanists, Watson (1871) was not altogether unaware of the questionable application of Pursh's name. He notes that Pursh's description differs from that given by Moquin-Tandon (1849, p. 164) "though both were drawn from Nuttall's specimens." Watson is, of course, wrong in this last regard. However, Moquin-Tandon does indicate in his 1849 account that he had seen a Nuttall specimen with the MS name "*Suaeda plattensis* Nutt." Presumably Moquin's description derives from it, for in 1840, when he had only the literature to guide him, he (rightly) cited *Salsola depressa* Pursh as a synonym of *Suaeda prostrata* Pallas. A Nuttall specimen collected at "R Mts Malta" (possibly Malta, Idaho or more likely an unidentified locality in Wyoming on the River Platte) with the manuscript name *Suaeda plattensis* is housed at BM*, and is probably the one seen by Moquin-Tandon. It is, in fact, neither *S. prostrata* nor *S. depressa* auct., but is referable to the perennial *S. torreyana* S. Watson, which explains some of the features of Moquin's description. This specimen must, of course, have been collected on Nuttall's 1834 expedition, long after the publication of *Salsola depressa* Pursh.

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*Abbreviations of herbaria follow *Index Herbariorum* ed. 6 (Holmgren & Keuken, 1974).

Selecting the correct specific epithet for the species hitherto called *Suaeda depressa* presents some problems. The next earliest name at specific rank that has been applied to plants of this species is *Chenopodium americanum* Sprengel (Syst. Veg. **1:** 922. 1824). After a three-line description applicable to almost any species of *Suaeda,* Sprengel's protologue states: "*Amer. boreal.* (Salsola salsa Pursh. Nutt. depressa Pursh.)". By implication the synonyms are: (1) *Salsola salsa* sensu Pursh, Fl. Am. Sept. 197. 1814, non L., Sp. Pl. ed. 2. 324. 1762; (2) *Salsola salsa* sensu Nutt., Gen. N. Am. Pl. **1:** 199. 1818, non L.; and (3) *Salsola depressa* Pursh, already discussed above. The first of these relates to a Michaux specimen from the mouth of the St. Lawrence River which happens also to be the type of *Suaeda americana* (Pers.) Fernald, although this name does not refer back, either directly or indirectly, to Sprengel's use of the epithet. The second comprises both this element and plants from the western plains. Current treatments recognize these as two species under the names *Suaeda americana* and *S. depressa.* The third synonym is the most critical nomenclaturally. Particularly relevant is the question of whether, in the light of Sprengel's geographic statement ("*Amer. boreal.*"), the citation can be interpreted as excluding the type of *Salsola depressa* Pursh, i.e., excluding *Suaeda prostrata* Pallas. Inasmuch as Sprengel's edition of the Systema vegetabilium seeks to enumerate and diagnose all known plant species, it is noteworthy that there is no reference anywhere in the work to *Suaeda prostrata* Pallas, other than this indirect one through *Salsola depressa* Pursh. This is so, even though he accounts for Pallas' other *Suaeda* species, and although Roemer and Schultes in the previous edition of the Systema vegetabilium had included this one as a distinct species doubtfully assigned to *Chenopodium.* Whatever one may feel was Sprengel's intention, there is no escape from the fact that he did cite *Salsola depressa* Pursh as a synonym with no explicit or implicit exclusion of its type. As such, under Article 63 of the International Code of Botanical Nomenclature (Stafleu *et al.,* 1972), the name was nomenclaturally superfluous when published and is automatically typified by the type of the epithet which ought to have been adopted under the rules, i.e., one of the two specimens from southern Russia upon which *Suaeda prostrata* Pallas is based.

In passing, it should be noted that even if this were not the case, the existence of *Suaeda americana* (Pers.) Fernald (Rhodora

9: 146. 1907) means that the epithet *americanum* Sprengel would be available in *Suaeda* only if it were typified through the first of its three synonyms. This would provide, as its type, the Michaux specimen, that is also the type of *Salsola salsa* var. *americana* Pers. (Syn. Pl. **1:** 296. 1805), the basionym of *Suaeda americana* (Pers.) Fernald, which is otherwise a nomenclaturally distinct use of the epithet. This is an isonym situation somewhat similar to that of *Alsophila kalbreyeri* discussed by Nicolson (1975).

In 1838, in Flora boreali-americana, Hooker described a *Chenopodium calceoliforme* on the basis of a Drummond specimen from near Carlton House Fort, (on the North Saskatchewan River, north of Saskatoon, Saskatchewan). On the basis of our examination of type material preserved at K and at NY, this refers to the western plains taxon to which the name *Suaeda depressa* has usually been applied. Its correct name at specific rank is, therefore, *Suaeda calceoliformis* (Hooker) Moquin.

The relevant citations of correct species name and synonyms for the western taxon long known as *S. depressa* are as follows:

Suaeda calceoliformis (Hooker) Moquin, Chenop. Monogr. Enum. 128. 1840.

Syn.: *Chenopodium calceoliforme* Hooker, Fl. Bor.-Am. **2:** 126. 1838.

Schoberia calceoliformis (Hooker) Moquin in DC., Prodr. **13**(2): 166. 1849.

(*Chenopodium americanum* Sprengel in L., Syst. Veg. ed. 16. **1:** 922. 1825, pro parte minore, typo excl.).

(*Suaeda prostrata* in Moquin, Chenop. Monogr. Enum. 130. 1840, pro parte, non (Pallas) Moquin).

(*Suaeda depressa* auct., non (Pursh) S. Watson quoad basionomen).

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BIOSYSTEMATICS RESEARCH INSTITUTE
AGRICULTURE CANADA
OTTAWA, CANADA K1A 0C6

APPENDIX

Pursh's description of *Salsola depressa* (Fl. Am. Sept. 197. 1814) is:

"4. S. herbacea, humifusa, ramosissima; ramulis distichis, foliis succulentis linearibus acutis glabris, floribus axillaribus sessilibus, staminibus exertis."

This can be compared with the diagnosis and selections from the description of *Suaeda prostrata* in Pallas (Ill. Pl. 55. *pl 47.* 1803) which read as follows:

"S. annua humifusa ramosissima, ramulis distichis, foliis succulentis acutis. . . .
Folia exigua, succulenta, lineari-acuta, glabra.
Flores in alis, foliorum (non omnium) sessiles . . .
. . . ; *stamina* exserta, . . ."

OBSERVATIONS ON TETRAMEROUS DISC FLORETS IN THE COMPOSITAE

ROBERT C. GARDNER

During the course of a systematic study of the genus *Lipochaeta* DC. (Compositae, Heliantheae) from the Hawaiian Islands, it was noticed that certain species are characterized by having four-lobed disc corollas and four anthers (referred to as tetramerous disc florets), while other taxa have typically five-lobed disc corollas and five anthers (pentamerous disc florets). These observations have led to an interest in the occurrence of the tetramerous condition within the Compositae and its taxonomic significance. The present paper attempts to improve our understanding of this phenomenon by: (1) summarizing the known distribution of the tetramerous condition of disc corollas within the family; (2) commenting on the possible ontogenetic and genetic factors influencing corolla lobe number; (3) offering suggestions for possible adaptive significance of the change to the tetramerous state; and (4) discussing the taxonomic significance of the tetramerous condition within different groups of the family.

DISTRIBUTION WITHIN THE FAMILY

The occurrence of tetramerous disc florets within the Compositae is relatively wide-spread, having been reported for more than 80 genera in nine of the 13 tribes (Table 1). The important points of the information presented in Table 1 are that the tetramerous condition occurs within many separate evolutionary lines, and that frequently both tetramerous and pentamerous florets are found in the same genus. Although reported for a few genera, this phenomenon is not common in the discoid or ligulate tribes. There is no apparent correlation between the occurrence of the tetramerous state and geographical distribution, as this condition is found almost equally in taxa of both the tropical and the temperate areas of the world.

ONTOGENY AND GENETICS

Floret development has been studied in several Compositae genera: e.g., *Aster* and *Solidago* (Martin, 1892); *Chrysanthemum*

Table 1. **Genera of the Compositae possessing tetramerous corollas** [a]

Genus	Number of Corolla Lobes [a]	Number of Species [b]
Vernonieae		
Rolandra Rottb.	4	1
Spiracantha Kunth	4, 5	1
Struchium P. Br.	3, 4	1
Eupatorieae		
Kanimia Gardn.	4	14
Astereae		
Bellis L.	4, 5	7
Bellium L.	4, 5	3
Calotis R. Br.	4[c]	20
Dicrocephala DC.	4, 5	13
Egletes Cass.	4, 5	12
Grangea Adans.	4, 5	6
Grangeopsis H. Humb.	4[c]	1
Keysseria Lauterbach	4	15
Laestadia Kunth	4, 5	6
Microtrichia DC.	4, 5	1
Myriactis Less.	4[c]	12
Psiadiella H. Humb.	4[c]	1
Remya Hillebr.	4[c]	2
Rhynchospermum Reinw.	4, 5	1
Thespis DC.	4	1
Inuleae		
Angianthus Wendl.	4, 5	30
Athroisma DC.	4	8
Epaltes Cass.	3–5	15
Evax Gaertn.	4, 5	15–20
Filago L.	4, 5	50
Gnephosis Cass.	4, 5	12
Micropsis DC.	4, 5	5
Millotia Cass.	4, 5	4
Myriocephalus Benth.	3, 4	10
Nanothamnus T. Thoms.	4	1
Quinetia Cass.	4, 5	1
Rutidosis DC.	4, 5	7
Sphaeranthus L.	4, 5	40
Stuartina Sond.	4, 5	2
Stylocline Nutt.	4[d]	6
Symphyllocarpus Maxim.	4	1
Thespidium F. Muell.	4	1
Toxanthes Turcz.	4, 5	2

Table 1 (Continued)

Genus	Number of Corolla Lobes[a]	Number of Species[b]
Heliantheae		
Abasoloa La Lave	4	2
Adenocaulon Hook.	4, 5	5
Coreopsis L.	4, 5[c]	120
Eclipta L.	4, 5	4
Glossocardia Cass.	4	2
Lantanopsis Wright	4	2
Lindheimera A. Gray & Englm.	4, 5	1
Lipochaeta DC.	4, 5[f]	28
Moonia Arn.	4[g]	1
Oparanthus Sherff	4[h]	2
Petrobium R. Br.	4[i]	1
Riencourtia Cass.	4, 5	8
Sclerocarpus Jacq.	3–5	15
Spilanthes Jacq.	4, 5	60
Synedrella Gaertn.	4	50
Thelesperma Less.	4, 5	12
Trichospira Kunth.	4	1
Helenieae		
Amauria Benth.	4[j]	3
Closia Remy	4	10
Correllia Powell	4[j]	1
Eutetras A. Gray	4[j]	2
Helenium L.	4, 5	40
Laphamia A. Gray	4	20
Lasthenia Cass.	4, 5[k]	16
Pericome A. Gray	4	4
Perityle Benth.	4	25
Rigiopappus A. Gray	3, 4	1
Thymopsis Benth.	4	2
Anthemideae		
Abrotanella Cass.	4	14
Centipeda Lour.	4	4
Ceratogyne Turcz.	3, 4	1
Cotula L.	4	80
Elachanthus F. Muell.	3, 4	1
Isoëtopsis Turcz.	4	1
Lidbeckia Bergius	4	2
Matricaria L.	4, 5	4
Nanothea DC.	4	1
Peyrousea DC.	4, 5	2

Table 1 (Continued)

Genus	Number of Corolla Lobes[a]	Number of Species[b]
Anthemideae (Cont.)		
Plagiocheilus Arn.	4, 5	7
Schistostephium Less.	4	12
Soliva Ruiz & Pav.	4	9
Thaminophyllum Harv.	4	2
Senecioneae		
Eriothrix Cass.	4, 5	2

[a]Bentham & Hooker, 1873. The list of genera was compiled mainly from this source, although especially large genera (*Vernonia*, 1000 spp., *Erigeron*, 200 spp., *Helichrysum*, 500 spp., and *Centaurea*, 600 spp.) were excluded because of the apparently infrequent occurrence of tetramerous corollas in these taxa. Representative specimens of most of the genera were examined by the author and additional data were added from the articles cited below.

[b]Harborne *et al.*, in press; this is the total number of species comprising the genus.

[c]Grau, in press.

[d]Correll & Johnston, 1970.

[e]Smith, 1972.

[f]Gardner, unpubl.

[g]Stuessy, 1975.

[h]Stuessy, in press a.

[i]Stuessy, in press b.

[j]Powell & Turner, 1974.

[k]Ornduff, 1966.

(Popham, 1963); *Lactuca* (Jones, 1927); *Tagetes* and *Tragopogon* (Sattler, 1973). Generally, the first stage of corolla development can be seen as five protuberances around the margin of a floret primordium. The tube is formed by intercalary growth of cells below these protuberances. As the corolla elongates, stamen primordia develop alternate to the lobes, with further elongation resulting from intercalary growth below the stamen primordia (Esau, 1965). Florets are initiated acropetally until all available space on the receptacle is occupied (Popham, 1963). Presumably, this generalized developmental sequence also could be observed in tetramerous disc florets, but I know of no study which provides such documentation.

In many Compositae one can observe an occasional tetramerous disc floret in a predominantly pentamerous capitulum. This possibly can be explained in terms of the crowding of floral

primordia. Apparently the number of florets initiated is a function of the receptacle size and whenever the space from one primordium to an adjacent one is sufficiently small, four lobes develop rather than five (R. A. Popham, personal comm.). This explanation also could be applied to the situation seen in heads with predominantly tetramerous disc corollas. In these taxa it is possible that there has been an increase in the number or size of the floral primordia, without a proportional increase in apex size, resulting in crowding of florets and the initiation of four lobes rather than five. The tetramerous species of *Lipochaeta* produce from 70% to 100% four-lobed disc corollas. In those taxa which do not produce all tetramerous florets, 70% of the pentamerous ones are found in the outer two whorls of the disc. At the time of floret initiation there could be slightly more space available toward the outside of the head. If there is more space, one might expect more pentamerous disc florets to develop there. The need for developmental studies to help understand how and why tetramerous disc florets develop seems apparent.

As for the genetic factors regulating corolla lobe number, it is possible that in at least some taxa the morphological change in number of corolla lobes and stamens is a mechanical consequence of polyploidy. Within *Lipochaeta,* 10 of the included species have tetramerous disc florets while the remaining 18 are pentamerous. Two different ploidy levels are found within the genus; $n = 15$ and $n = 26$. Preparations of cells from the higher numbered group show 26 bivalents with from one to four much smaller dark-staining bodies. These bodies are interpreted as centric fragments, indicating an aneuploid reduction from the tetraploid number of $n = 30$. To date, 15 of the 28 species have been determined chromosomally (Gardner, unpubl.). Of these, eight are diploid, while seven are tetraploid. The diploids uniformly have pentamerous disc florets and the tetraploids are consistently tetramerous. In *Lipochaeta,* there is an obvious relationship oetween polyploid level and number of corolla parts. Experimental studies designed to ellucidate the connnection between these two features are needed.

POSSIBLE ADAPTIVE SIGNIFICANCE

Very little has been written about tetramerous disc florets in the Compositae, and therefore, there is next to no information on

the adaptive significance of this morphological change. Some speculations, however, might be useful at this time.

First, one might speculate that a change from the pentamerous to the tetramerous condition is related to a change in breeding system from chasmogamy to autogamy. Assuming no other morphological alterations, a floret with four anthers would produce less pollen than one with five anthers. If less pollen is required to insure fertilization within a selfing head as compared to one that is outbreeding, such a change would result in a more energetically efficient system. This has been shown to be the case in *Lasthenia* of the Helenieae (Ornduff, 1966). Along with numerous other morphological changes, the self-pollinating tetramerous Lasthenias produce less pollen per floret than their outbreeding pentamerous relatives. With respect to *Lipochaeta,* reduced pollen production does not seem to be correlated with tetramerous disc florets. Comparisons of pollen grain number estimates show that the tetramerous Lipochaetas produce as many or more grains per floret than the pentamerous species. Little is known, however, about the breeding systems within the genus.

Second, it is possible that a change from the pentamerous to the tetramerous state can be explained in terms of selective pressures for increased reproductive potential. In *Lipochaeta,* the tetramerous taxa, on the average, produce ten more florets per head than the pentamerous species. As discussed in a previous section, tetramerous disc florets might result when the distance from one floral primordium to an adjacent one is sufficiently small, this reduced distance from one floret to the next resulting in more florets, i.e., more seeds, produced per head. This idea would fit into Stebbins' (1974) "line of least resistance" theory. That selective pressures for increased reproductive potential have existed (and still do exist) in *Lipochaeta* can be inferred from a consideration of the relative success of the tetramerous vs. pentamerous taxa. With the exception of two species (out of 18), each of the five-lobed Lipochaetas has a very restricted distribution, e.g.: *L. exigua,* two localities in the Hoary Head Range of Kauai; *L. waimeaensis,* a single gulley on the west side of Waimea Canyon of Kauai; *L. kamolensis,* Kamole Gulch on southern East Maui; etc. The tetramerous species on the other hand are very common, many of them becoming weedy in certain areas, e.g.: *L. rockii,* known from several localities on central Molokai

through the west end of that island; *L. heterophylla,* commonly encountered on three different islands, Molokai, Maui, and Lanai; *L. lobata,* very common around Kaena Point and from Diamond Head to Waimanolo Beach on Oahu. Assuming the chances for seedling survival are the same, the success of the latter species could be due in part to greater seed production.

TAXONOMIC SIGNIFICANCE

The usefulness of a consistent morphological feature (e.g., the number of floret parts) as a taxonomic character is dependent upon its proven efficacy in a particular instance. In the case of the tetramerous condition, its taxonomic utility, in combination with other useful characters, is known from the subtribal to the infraspecific level. The subtribe Peritylinae of the Helenieae is characterized by having genera that are primarily tetramerous (Powell & Turner, 1974). In *Coreopsis* (Smith, 1972, 1975) and *Lipochaeta* (Gardner, unpubl.) tetramerous disc florets are significant at the sectional level. In the previously mentioned work of Ornduff (1966) with *Lasthenia,* the number of corolla lobes is a useful character at the specific and infraspecific levels.

The occurrence of four-merous corollas is not only significant for descriptive taxonomy but is also valuable for constructing phylogenetic schemes. As evidenced by its rarity (present in only about 80 or 1250 genera), the tetramerous character state is probably derived within the entire family. In addition, detailed studies on individual genera such as *Coreopsis* (Smith, 1975), *Lasthenia* (Ornduff, 1966), and *Lipochaeta* (Gardner, unpubl.), indicate a derived status for the tetramerous condition within these taxa. It is realized that evolutionary reversals might have occurred from the tetramerous back to the pentamerous state, as is known to happen in other apparently directional features (Eyde, 1971; Stebbins, 1975), but it is hoped that this evaluation will alert other workers to the potential of this feature in determining evolutionary trends within the groups they study.

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DEPARTMENT OF BOTANY
THE OHIO STATE UNIVERSITY
COLUMBUS, OHIO 43210

VERNONIA (COMPOSITAE) IN THE BAHAMAS — REEXAMINED

STERLING C. KEELEY AND SAMUEL B. JONES, JR.

The flora of the Bahamas, as originially described by Britton and Millspaugh in 1920, included a large number of purportedly endemic species. However, in the early part of this century little was know of the causes or the extent of variation in natural populations; consequently some of the taxonomic treatments of that time were based on distinctions more apparent than real. Specific rank was often assigned on the basis of geographical location, particularly where islands were involved, rather than on any clear-cut morphological differences. Many of these species have since been shown to be insular representatives of mainland types and not truly endemic (Gillis 1974, 1975).

The treatment of *Vernonia* in Britton and Millspaugh (1920) was based on a paper by Gleason (1906) in which he distinguished several closely related taxa in sect. *Lepidaploa,* subsect. *Scorpidae* series *Reductae: V. arctata,* later synonymized to *V. arbuscula* Less. (Gleason 1922); *V. bahamensis* Griseb.; and *V. obcordata* Gleason. In the same paper, he also described a new species in subsect. *Paniculatae, V. insularis* Gleason.

Within series *Reductae* the three similar appearing taxa were distinguished primarily on the basis of leaf size and shape (Table l). Gleason maintained that *Vernonia arbuscula* could be distinguished from *V. bahamensis* by its shorter broader leaves, more crowded branches and more numerous heads. The geographical distribution of these two species was reported to be non-overlapping, with *V. bahamensis* occurring in the more southerly islands. The third species, *V. obcordata,* was characterized by leaves as broad as long, obcordate at the apex, and a yellow pappus.

Vernonia insularis of subsect. *Paniculatae* was described from several of the northern islands. Due to the similarity in appearance between this species and *V. blodgettii* Small, an endemic of southern Florida, Gleason felt they were closely related. *Vernonia cinerea* (L.) Less., a pan tropical weed of sect. *Tephrodes,* was reported as introduced in New Providence (Gleason, 1906).

Table 1.

Characteristics used by Gleason (1906) to distinguish V. arbuscula, V. bahamensis and V. obcordata.

Character	V. arbuscula	V. bahamensis	V. obcordata
Leaf length, cm	1–1.8	2–3.5*	0.8–1.5
Leaf width, cm	0.6–1.1	0.5–1.2	0.7–1.5
Petiole length, mm	3–7	*	5
Involucre height, mm	4–5	3–4	4–5
Number of flowers per head	13	8–13	8–13
Achene length, mm	2.5	2–2.5	—
Inner pappus length, mm	5	4–5	—
Location:	New Providence Island	Fortune and Inagua Islands	Little Inagua Island

*Included in leaf length

Ekman (1914) examined the Bahaman Vernonias as part of his revision of the Vernonieae of the West Indies and accepted Gleason's treatment (1906) as substantially correct. Ekman pointed out that there was a close resemblance between *Vernonia arbuscula* and *V. bahamensis*, but he felt that the number of lateral veins in the leaves and the angle at which they issued from the main vein were sufficient to allow separation of these two taxa.

Since the early work by Gleason collections of Bahaman *Vernonia* have increased in number and encompassed more of the islands in the chain. Many of these specimens are difficult to identify using Gleason's criteria (Table 1), and have evidently been difficult to distinguish in the past. Many specimens have been annotated with at least two of the three possible specific epithets, and some have all three. In addition, the geographical distributions which in the past were used to separate the taxa, have become less distinct with the addition of new material, and these distinctions can no longer be used uncritically.

Geographical distribution strongly influenced taxonomic treatments in the early part of this century (Gillis 1974) and it is possible that the very similar appearing *Vernonia insularis* and *V. blodgettii* are actually conspecific, but this likelihood has not been examined. In short, the taxonomic status of these Vernonias is in need of review since the taxa are not well understood.

MATERIALS AND METHODS

Loans of herbarium material were obtained from US, NY, TEX, GH, MO, and F. Taxa were also grown and maintained in the greenhouse at UGA and used during this study for cytogenetic work and morphological comparisons.

Twenty-five specimens were selected from a group containing putative *Vernonia arbuscula, V. bahamensis,* and *V. obcordata* since many specimens have been annotated with at least two epithets. In addition, all specimens annotated by Gleason or identified by him in his 1906 paper were separated by species and scored. Each specimen was measured for the following characters: plant height, length and width of the leaf blade, ratio of length to width of the leaf blade, petiole length, involucre height, involucre width, inner phyllary length, inner phyllary width, number of flowers per head, number of achene ribs, achene length, inner and outer pappus length, corolla length and anther length. Midcauline leaves were selected for measurement on each specimen; only fully matured heads were used for measurements of length and width of involucres and phyllaries, anther length and corolla length were measured on soaked, fully mature flowers.

Trichomes, venation patterns, and epidermal cell patterns were examined from leaves of herbarium material representing all taxa as annotated by Gleason. Trichomes were observed from leaf scrapings in aqueous mounts and on safranin stained leaf fragments cleared by the method of Herr (1971).

Field and greenhouse grown specimens of *Vernonia insularis* and *V. blodgettii* were measured and scored separately. Crosses were made between these two taxa by the method of Jones (1972), and the pollen of the progeny was examined for fertility by staining with aniline blue. Chromosome figures were examined from pollen mother cells of greenhouse grown *V. insularis, V. blodgettii* and their hybrid progeny, using the standard aceto-carmine staining technique. Trichomes, venation patterns, and epidermal cell patterns of leaves from greenhouse grown plants were examined and compared with herbarium material. Plastic nail polish impressions were made from fresh leaves. Leaves from herbarium specimens were cleared and stained. Leaves from greenhouse accessions of *V. insularis, V. blodgettii* and their hybrids were analyzed for sesquiterpene lactones by Dr. M. Betkowski at the University of Texas.

RESULTS AND DISCUSSION

Subsection Scorpidae Series Reductae:

Gleason reported the number of flowers per head in *Vernonia arbuscula* to be 13 (Table 1), however, counts of three heads per specimen on 13 sheets annotated by Gleason revealed a range of 9 to 14. Other key characters used by Gleason such as achene length, involucre height and inner pappus length were also found to be too variable and hence not useful in classification.

Although the branches were reported to be crowded in *Vernonia arbuscula,* and the heads more numerous than in *V. bahamensis* (Gleason, 1906), this character did not appear to be consistent. Some specimens obviously were taken from terminal branches; the number of heads in these terminal branches also appeared to be a variable character reflecting the length of time, and perhaps the availability of favorable growing conditions rather than any fixed and therefore measurable character of the taxon. Some specimens annotated by Gleason as *V. bahamensis* also had numerous, crowded heads.

Only one specimen of *Vernonia obcordata,* described by Gleason, was available and it was the holotype. Several sheets from later collections had prominently obcordate leaves. The pappus color, on the type specimen, and on other specimens with obcordate leaves was not particularly yellow as Gleason (1906) had indicated. During examination of soaked corollas, the pappus bristles of all taxa often turned yellow upon drying; it is possible that this was the source of the reported color variation.

Of the several characteristics originally used by Gleason to distinguish the three species in series *Reductae,* only leaf size and shape, and shape of the leaf apex correspondingly associated with distinct geographical distribution appeared to provide tentative criteria for positive identification. In attempting to faithfully apply these criteria, however, it soon became apparent that leaf size, at least, was too variable to be used. Gleason did not specify which leaves he scored, i.e. cauline or bracteal, and the range in size of leaves on one specimen alone was often great enough so that it could have been classified in all of the three possible taxa.

Five leaves were randomly selected from each specimen and were placed into one of the three categories of leaf shape given

by Gleason (Figure 1, inset). This examination showed that leaf shape was also highly variable; and not geographically correlated (Figure 1). Of the 83 specimens examined, 43% had at least two leaf shapes and 18% had all three possible shapes.

A comparison of trichome complements revealed no differences between the taxa in this group. Uniserate, awl-shaped, awl-shaped glandular, L-shaped and T-shaped, glandular and non-glandular bilobed trichomes of Faust and Jones (1973) were observed. Stomata were found on both leaf surfaces. Venation patterns, reported to be distinctive by Ekman (1914), were found to vary with leaf size and were of little use in distinguishing taxa. The three taxa in the series *Reductae* should be reduced to a single variable taxon distributed throughout the Bahama Islands (Figure 2).

Subsection Paniculatae:

The means, standard deviations and range of representative morphological characteristics of field collected and greenhouse grown specimens of *Vernonia insularis* and *V. blodgettii* are shown in Figure 3. It is not possible to clearly differentiate field collected specimens of these two taxa on the basis of number of flowers per head, corolla length, anther length or involucre height and width. Although leaf size appears distinct in field collections, this difference is lessened when greenhouse grown specimens are included. This overlap indicates that leaf size is strongly influenced by environmental parameters and makes this character of dubious value for taxonomic determinations.

Vigorous and fertile first generation hybrids were produced from crosses between *Vernonia insularis* and *V. blodgettii* (Table 2). Examination of trichomes indicated that there were no consistent differences between parental accessions and/or their hybrids. Bilobed, awl-shaped glandular and L-shaped trichomes appeared in all specimens examined and stomata appeared on both leaf surfaces. No difference in epidermal cell size or shape, or venation patterns appeared in examinations of cleared leaf fragments from herbarium specimens.

Sesquiterpene lactone determinations indicated that *Vernonia insularis* contained glaucolide F and an unidentified sesquiterpene lactone, whereas *V. blodgettii* contained only glaucolide A. Glaucolides A and F differ by a single methyl group. Evaluation

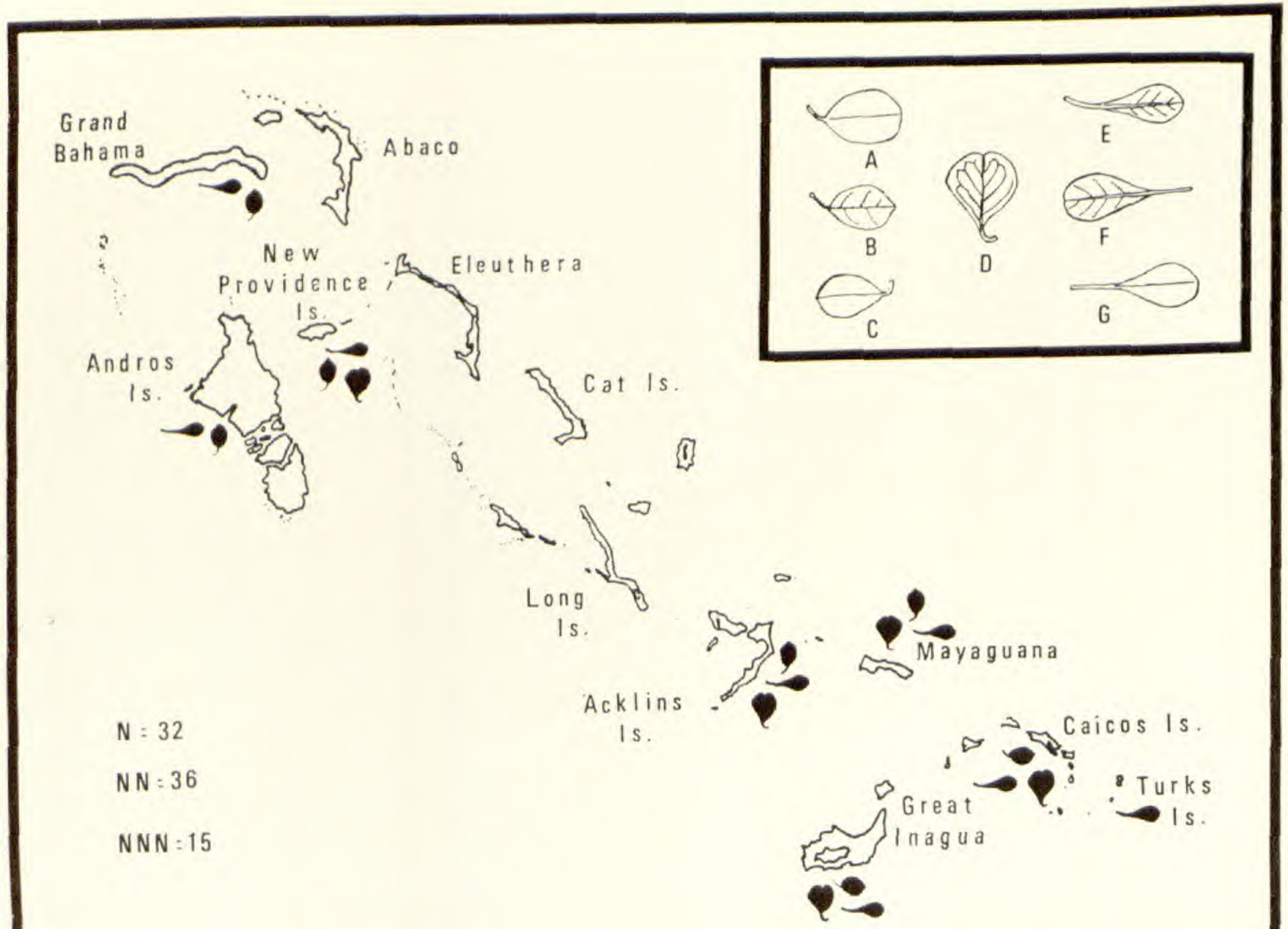

Figure 1 (inset). Leaf shapes used by Gleason to distinguish *Vernonia arctata* = *V. arbuscula* (A–C), *V. obcordata* (D), and *V. bahamensis* (E–G). Redrawn from Gleason (1906). The distribution of leaf type throughout the Bahama Islands for *Vernonia arbuscula* Less. N = the number of individuals with only one leaf shape, NN = the number of individuals with two leaf shapes and NNN = the number with all three leaf shapes.

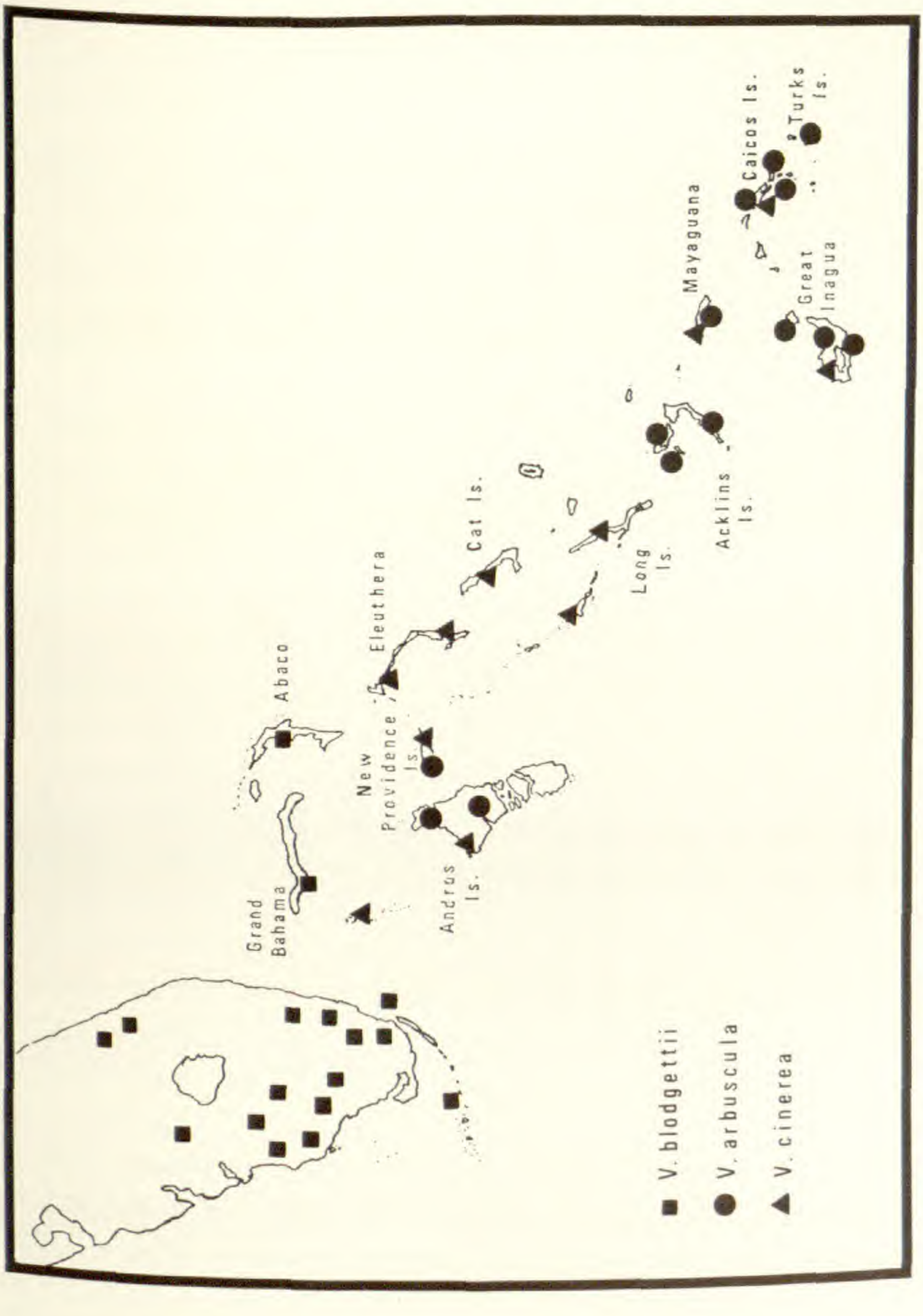

Figure 2. The distribution of *Vernonia blodgettii*, *V. arbuscula*, and *V. cinerea* in southern Florida and the Bahamas.

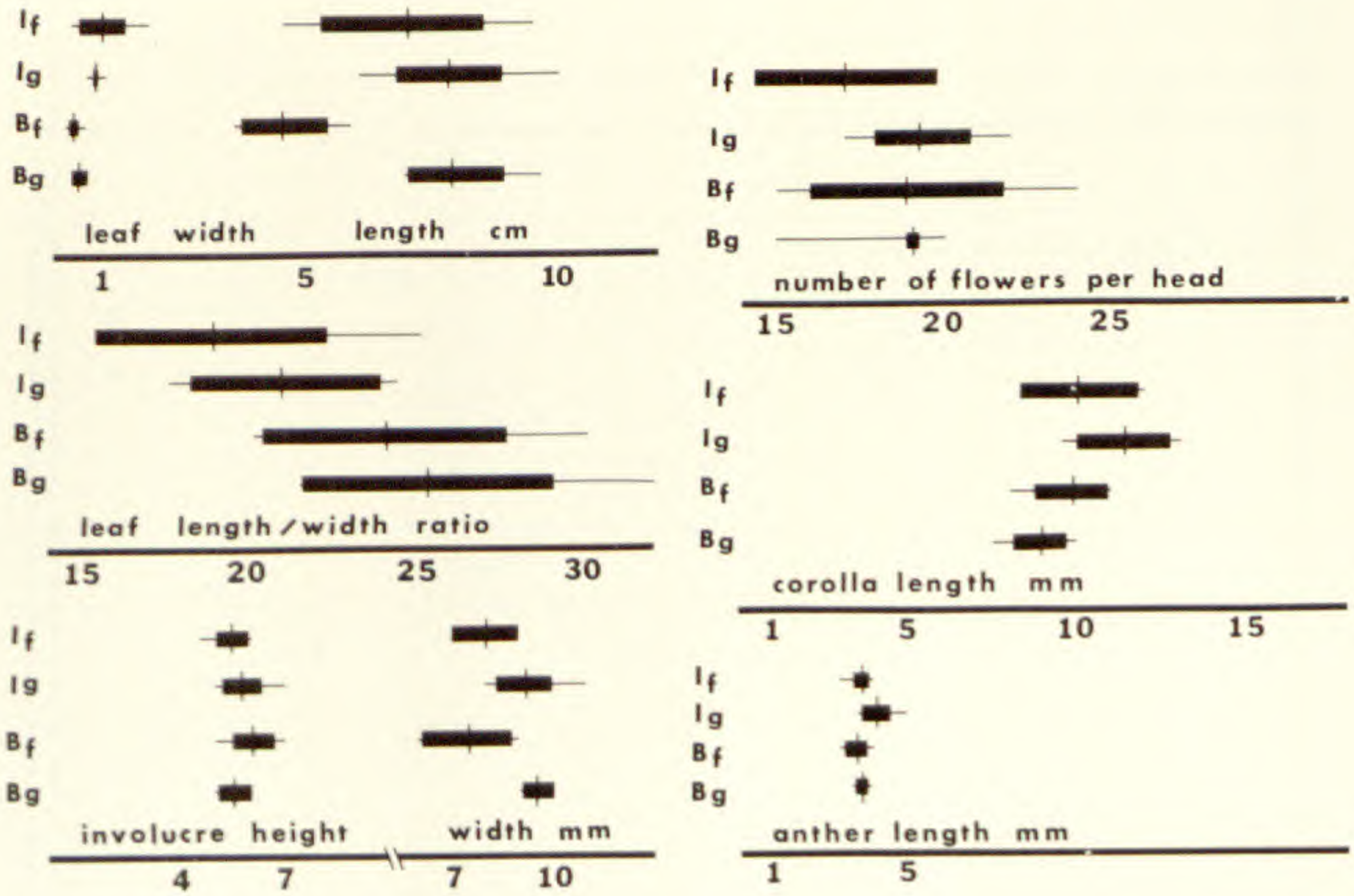

Figure 3. Selected morphological measurement of field collected *Vernonia insularis* (I_f), and greenhouse grown *V. insularis* (I_g), and field collected and greenhouse grown *V. blodgettii*, (B_f) and (B_g) respectively.

Table 2.

Summary of fertility in greenhouse accessions of V. insularis, V. blodgettii and their hybrids.

Taxa	Generation	Pollen Stainability Range	Mean
V. blodgettii	P_1	55–89	69
V. insularis	P_1	(64)92–97	91
Crosses			
V. insularis × *V. blodgettii*	F_1	95	95*
V. blodgettii × *V. insularis*	F_1	93–100	94
		56–95**	88

* 1 count only.
**Second year.

of these differences is very difficult, however, since nothing is known of the extent of variation in sesquiterpene lactones within these taxa. Additionally, inheritance of sesquiterpene lactones is variable and is not well understood (Herout, 1970; Burnett, 1974). In any case it is difficult to provide a rationale for distinguishing macroscopic organisms on the basis of chemical differences that require special training and a sophisticated laboratory to detect (Davis & Heywood, 1963; Alston & Turner, 1972).

As pointed out by Gillis (1974) many species occurring in the Bahamas have been considered to be unique in the past because they were isolated from related mainland populations. This distinction may be valid if there are morphological differences which allow clear recognition of distinct taxa. However, when there are no morphological differences distinguishing the mainland groups from insular representatives there is little justification for maintaining separate taxonomic status, particularly when the individuals from each of the two areas are interfertile and produce viable and vigorous F_1 hybrid plants.

Dispersal and potential exchange of genes in nature has not been studied in these taxa; however, it cannot be overlooked. For example, the distance between Florida and the island of Abaco is scarcely 50 miles and well within the range of seed transport (Thorne, 1972). Thorne (1972) and McNeil and Burton (1973) have shown that wind and hurricanes, and bird migrations (which occur from Florida to the Bahamas) provide ready dispersal agents. If two mainland populations of a species were

separated by this distance or a greater one, but were morphologically indistinguishable they would hardly be considered subspecies let alone distinct species. Recognition of disjunct species too, would scarcely be possible if geographical distance were taken as the main criteria for distinguishing species. Although the geographical range of this taxon includes an island, a separate specific designation would prejudge the evolutionary status and existence of a unique colonizing event by this taxon.

If systematists are to provide a working framework for biogeographers and others to use in understanding island floras, then perhaps the greatest service we can render is to avoid the historical pitfalls of island botanists and point out morphological and genetic similarity where it exists. To this end the following taxonomic revision is proposed:

KEY TO TAXA

a. Plants perennial.
  b. Fructicose to woody plants; flowers 8–12 per head; leaves 1–4 cm long, 0.82 cm wide. ..... 1. *V. arbuscula* Less.
  b. Herbaceous plants; flowers 15–25 per head; leaves 6–10 cm long, 0.5–1 cm wide. ..... 2. *V. blodgettii* Small.
a. Plants annual, flowers 12–16 per head; leaves 2–5 cm long, 1.5–2.5 cm wide. ..... 3. *V. cinerea* (L.) Less.

1. **Vernonia arbuscula** Less., Linnaea **6:** 664. 1831. TYPE: **Mauritius** (error): *Salisbury 1816* (Holotype, destroyed at Berlin; neotype, here designated: **Bahamas,** near Nassau, *Curtiss 65* (US!)).

Vernonia arctata Gleason, Bull. Torrey Bot. Club **33:** 185. 1906. TYPE: **Bahamas:** near Nassau, New Providence, *Curtiss 65* (Isolectotypes: F! GH! US! MO!).

Vernonia obcordata Gleason, Bull. Torrey Bot. Club **33:** 187. 1906. TYPE: **Bahamas:** Inagua, *Nash & Taylor 1206* (Holotype: F!).

Vernonia bahamensis Griseb., Fl. Brit. W. Ind. 352. 1861. TYPE: **Bahamas:** *Brace 23/9/77* (Holotype: K!).

Cacalia bahamensis (Griseb.) Kuntze, Rev. Gen. 969. 1891.

Shrub up to 3 m tall; stems gray to brown tomentose, glandular dotted, often much branched at least terminally. Leaves crowded, especially on terminal branches, leaf blades 1.5–2(4) cm long, 0.6–1.5 (2.2) cm wide (length/width ratio ca. 1.5) widest above the middle, spatulate, obovate, obcordate, to lanceolate, surface gray-green tomentose, gland dotted, upper surface frequently

darker than lower, often greener in appearance than lower surface which occasionally appears whitish. Leaves apically acute to blunt, retuse, emarginate to obcordate, basally tapering, margins entire to repand, petioles 6–8 mm long, grey-brown tomentose, glandular. Inflorescences much condensed on terminal cymes, usually with 3–5 heads. Heads 8–12 flowered, sessile, usually subtended by a small leaf. Involucres campanulate, 4–5 mm high, 4–5 mm wide; phyllaries tomentose to villous, closely appressed when immature, golden brown in color; inner phyllaries awl-shaped, tomentose to villous, with conspicuous resinous dots, 3.5–4 mm long, 1–1.5 mm wide, tips tapering, acute; outer phyllaries broadly awl-shaped, densely pubescent, size variable with age. Pappus whitish to straw colored; inner bristles 5–6 mm long, outer pappus scales 0.5–1 mm long, edges jagged often deeply cleft. Corollas 6–9 mm long, violet to rose-purple, smooth surface, little or no odor. Anthers (1.5) 2.5–3.2 mm long. Achenes 2–3.5 mm long, sericeous to hirsute, hairs shiny, 5–10 ribs 5 large, 10 smaller. $n = 17$. Flowering and fruiting all year.

This species is distributed throughout the Bahama Islands, in pinelands, and limestone barrens. It is a highly variable species, particularly with regard to leaf shape (Figure 1).

Ekman (1914) saw the original type specimen of *Vernonia arbuscula* during a visit to Berlin prior to 1914. He pointed out that it was the same as *V. arctata* Gleason and cited several specimens of *V. arctata* which he had seen; among these specimens was that of *Curtiss 65*. In 1922 Gleason reduced *V. arctata* to synonymy with *V. arbuscula*. Since Ekman had seen both Lessing's type of *V. arbuscula* and several specimens described by Gleason as *V. arctata* including *Curtiss 65*, it seems a logical choice for the Neotype.

REPRESENTATIVE SPECIMENS: **Bahamas:** Acklin's Island, *Brace 4330* (NY, US); Crooked Island, *Rothrock 276* (F); Mariguana, *Wilson 746* (NY, F, GH); Great Inagua, *Nash & Taylor 1017* (F, NY); Turks Islands, *Millspaugh & Millspaugh 9362* (F, NY, GH); Caicos, *Wilson 7721* (NY, F); New Providence, *Wight 70* (NY, F, GH); Andros, *Brace 6926* (F, NY); Castle Island, *Wilson 7783* (NY, F, GH); Fortune Island, *Eggers 3832* (NY, US).

2. **Vernonia blodgettii** Small, Fl. S. E. U. S. 1160. 1903. TYPE: **Florida:** Pine Key, Monroe County, *Blodgett* (Holotype: NY!).

Vernonia angustifolia Michx. var. *pumila* Chapm., Bot. Gaz. **3:** 5. 1878. TYPE: same as for *Vernonia blodgettii*.

Vernonia insularis Gleason, Bull. Torrey Bot. Club **33:** 184. 1906. TYPE: **Bahamas:** Great Bahama, *Britton & Millspaugh 2392* (Holotype: NY!).

Stems erect, glabrous, often branches at base, 2–5 dm tall. Leaves mostly basal, 1.8–6.9 cm long, 0.1–1.0 cm wide, linear or nearly so, glabrous above, lightly glandular dotted below, tips obtuse to acute, attenuate at the base, margins slightly revolute, entire. Inflorescence loose, irregular, with few heads. Heads about 21-flowered. Involucre loosely and irregularly imbricated, campanulate, 5–8.5 mm high, 5.5–10.5 mm wide. Bracts deltoid to lanceolate, inner 3.9–6.7 mm long, outer 1.7–3.5 mm long, purple, glabrous to slightly pubescent. Bract tips acute to subacute, 0.1–0.5 mm long. Achenes pubescent, ribbed, 2.3–2.7 mm long. Pappus light yellow, bristles 5.5–7.8 mm long, scales irregular, 0.5–0.8 mm long. $n = 17$.

REPRESENTATIVE SPECIMENS: **Bahamas:** Abaco: *Gillis 7737* (GA), *Robertson 330* (GH); *Proctor 3043* (TEX); *Brace 1835* (NY); Grand Bahama: *Brace 3683* (F, NY); *Britton & Millspaugh 2392* (NY). **Florida:** Indian River Co.; *Small 8882* (NY); Brower Co. *Small 1634* (NY); Charlotte Co.; *Jones 1101* (GA). For a complete list of Florida localities see Jones (1964a).

3. **Vernonia cinerea** (L.) Less., Linnaea **4:** 291. 1829. TYPE: No location given (LINN, IDC microfiche!).

Conyza cinerea L., Sp. Pl. 862. 1753.
Cacalia cinerea (L.) Kuntze, Rev. Gen. Pl. 323. 1891.
Seneciodes cinereum (L.) Kuntze ex Post & Kuntze, Lex. Gen. Phan. 515. 1904.

Annual; stems tomentulose with T-shaped hairs sometimes becoming glabrate with age below and tomentulose with T-shaped hairs above, 3–6 dm high; leaves scattered along stem; blades of middle stem leaf 1.5–2.5 cm wide, 2–5 cm long, lanceolate, pubescent above, pubescent with T-shaped hairs, and punctate beneath, apically acute, basally attenuate, margins remotely toothed; petioles margined, ca. 1.5–2.5 cm long, pubescent; inflorescence loose, open and often spreading; heads 12–16 flowered; involucre campanulate, 6–7 mm high, 5–6 mm wide; phyllaries loosely and irregularly imbricate; inner phyllaries linear-oblong, 5–5.5 mm long, 0.6–0.8 mm wide, with acuminate to subulate purplish tips 0.5–1 mm long; pappus whitish, deciduous; inner bristles ca. 4 mm long; outer bristles ca. 0.2 mm long; corollas purplish-lavender, 6–7 mm long; achenes rounded, nearly ribless, ca. 1.5 mm long; flowering the year around. $n = 9$.

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DEPARTMENT OF BOTANY
UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30602

JUNCUS TRIGLUMIS IN NORTH AMERICA

FREDERICK J. HERMANN AND WILLIAM A. WEBER

In 1924 Fernald pointed out that Lange's *Juncus triglumis* var. *albescens* (Conspect. Fl. Groenl. 123. 1880) was actually specifically distinct from var. *triglumis* and concluded from his review of North American collections of the group that all of our material was referable to *J. albescens* (Lange) Fern. and that *J. triglumis* L. was strictly Eurasian. Evidently he saw few collections from the Rocky Mountains (he cited only three from Colorado) as it is now clear that both species occur there. This was first noted by the junior author, fortunately in time for inclusion of both species in the 5th edition of *Rocky Mountain Flora* (Weber, 1976) but not soon enough for *J. triglumis* to be included in *Manual of the Rushes* (*Juncus* spp.) *of the Rocky Mountains and Colorado Basin* (Hermann, 1975). It now seems desirable to establish the distribution of *J. triglumis* in North America as a whole.

In 1939 Porsild reported the occurrence of both *Juncus albescens* and *J. triglumis* in Alaska. Hultén (1968) treated *J. albescens* as a subspecies of *J. triglumis.* His distribution map for subsp. *triglumis* shows it as occurring in northern Alaska, northernmost Canada and Greenland, as well as in Eurasia.

Hitchcock (in Hitchcock, C. L., A. Cronquist, & M. Ownbey, 1969) regarded *Juncus albescens* as "a New World race, var. *albescens* Lange" and referred to *J. triglumis* var. *triglumis* as Eurasian.

To us, *Juncus albescens* appears to be sufficiently differentiated from *J. triglumis* (as it did to Fernald and Porsild), to merit specific rank. The characteristics enumerated in the following key, modified from that in Fernald's discussion, are well illustrated in Fernald's *Plate 249,* Rhodora **35,** 1933. Moreover, the junior author has observed that the two taxa are found in quite different habitats, as indicated in the present key. In addition to the key characters, *J. albescens* shows a strong tendency to have a much paler perianth, and sometimes the bracts as well are distinctly whitish (hence the epithet *albescens*), but occasional plants will have the perianth as dark as in *J. triglumis,* apparently due to age and/or soil or exposure. In arctic Alaska the culms of *J. triglumis* tend to become much more elongated than elsewhere in its range, occasionally even equaling those of *J. albescens.*

KEY TO JUNCUS TRIGLUMIS & JUNCUS ALBESCENS

Culms mostly 4.5–8 (35) cm high; *bracts* usually obtuse or the lower mucronate, generally conspicuously shorter than the flowers; *mature capsule* 4.5–7 mm long, conspicuously exserted from the perianth, firm, castaneous and conic to rounded below the short beak; *mature seeds* (including tails) 1.75–3 mm long; plant of wet gravels of snow melt basins of high altitudes. . . . *J. triglumis* L.

Culms mostly 6–35 cm high,more slender; *bracts*, at least the lower, long-acuminate or long-awned and equal to or overtopping the lowest flower; *mature capsule* 3–5 mm long, included or barely exserted from the perianth, thinner and paler, rounder to subtruncate at summit; *mature seeds* 1.25–2 mm long; plant of peat bogs. . . . . *J. albescens* (Lange) Fern.

In the Colorado mountains *Juncus triglumis* is the more common of the two taxa. The only intermediate station for it between the Colorado mountains and Alaska appears to be Park County, Wyoming, in the Beartooth Mountains. Porsild (1939) says of its Alaskan distribution: "In Alaska *J. triglumis* appears to be less common than *J. albescens*. It is the more arctic-alpine of the two and along the north coast of Alaska reaches a short distance east of the Mackenzie where *J. albescens* is absent. *J. triglumis*, unlike *J. albescens*, is not limited to calcareous soils." Material examined from the herbaria of the Rocky Mountain area and the National Museum of Canada indicates that *J. triglumis*, besides being frequent to locally common in Eurasia, occurs in North America, in the mountains of Colorado, the Beartooth Range in northwestern Wyoming, in arctic Alaska (with one outlying station in the Alaska Range of central Alaska), the Yukon, and the extreme northwest of the Northwest Territories.

REPRESENTATIVE SPECIMENS

Colorado: BOULDER CO., edge of swale on tundra, Nowit Ridge, 11,500 ft., ca. 8 mi. NW of Nederland, *Hermann 17055* (US, USFS); cirque of Arapaho Glacier, 11,000–11,600 ft., *Komarkova*, Aug. 12, 1972 (COLO); Upper Coney Lake, 10,900–11,200 ft., *Komarkova*, July 22, 1972 (COLO); Lake Envy, in cirque of Middle St. Vrain Creek Valley, 11,000 ft., *Komarkova*, Aug. 9, 1972 (COLO). GRAND CO., Pawnee Lake Cirque, 10,800–11,450 ft., *Komarkova*, Aug. 4, 1972 (COLO). LARIMER CO., wet gravels of tundra W of Lawn Lake, Mummy Range, 12,000 ft., *Willard 62186* (COLO). PARK CO., boggy basin S side of Hoosier Ridge, 11,500 ft., (solifluction lobes) *Weber 7912* (COLO). SUMMIT CO., cirque on E slope of North Star Mt., 11,500–12,250 ft., *Komarkova*, Aug. 9, 1973 (COLO).

Wyoming: PARK CO., solifluction terrace, head of Wyoming Creek, 10,700 ft., Beartooth Range, *Johnson 1873 & 2358* (RM).

Alaska: moss-sedge swamp, Tangle Lake, mts. E of Landmark Gap, Alaska Range, *Gjaerevoll 1292* (CAN); emergent hydrophyte in peat bog, Sadlerocket River, 1,500 ft., arctic N slope of Alaska, *Spetzman 1049* (CAN).

Yukon Territory: mossy seep, vicinity of Mackintosh, Mile 1,035, Alaskan Highway, southwest Yukon, *Schofield & Crum 7745* (BC); flooded depressions on valley floor, St. Elias Mts., Steele Glacier & vicinity, 5,500–7,000 ft., *Murray & Murray 1302* (CAN).

Northwest Territories: 6 miles E of Kittigazuit, ca. 69° 20′N, 133° W, arctic coast, *Porsild & Porsild 2543* (CAN); bald, windswept summit of Mt., Plains of Abraham, ca. 6,000 ft., Mile 82, Canol Rd., Mackenzie Range, *Porsild & Breitung 11796* (CAN).

ACKNOWLEDGMENTS

We wish to thank the curators of the following herbaria for the loan of specimens: ALTA; BC; CAN; CS; ID; IDS; MONTU; RM; UT; UTC; WTU.

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F. J. H.
FOREST SERVICE HERBARIUM, USDA
240 W. PROSPECT ST.
FORT COLLINS, COLORADO 80521

W. A. W.
UNIVERSITY OF COLORADO MUSEUM
BOULDER, COLORADO 80302

REDISCOVERY OF PSILOCARYA NITENS IN NEW ENGLAND[1]

BRUCE A. SORRIE

One of the rarest, if not the rarest member of the New England flora is the bald-rush *Psilocarya nitens* (Vahl) Wood, whose precarious existence here is verified by a single collection from Massachusetts in the New England Botanical Club Herbarium. This collection consists of a single sheet containing but one plant. The label reads "muddy shore, West Pond, Plymouth, Sept. 13, 1925, L. B. Smith & F. E. Smith, Jr." There is no collection number.

This find was reported briefly in Rhodora **28:** 88; and as recently as 1963 the NEBC Committee on Plant Distribution stated that this remains ". . . the only New England station yet discovered" (Rhodora **65:** 33). *Psilocarya nitens* is only of local occurrence throughout most of its range from eastern Texas to Florida north to southern New Jersey, with outlying stations on Long Island, N. Y., in Plymouth, Mass., and an isolated colony in the dunes of northwestern Indiana. Nonetheless, the frequency with which suitable habitat occurs in the pine-oak barrens of southeastern Massachusetts and on Cape Cod suggests that this species should be found at more than one site.

During the summer of 1975, while conducting field work in the area, I found *Psilocarya nitens* growing on the borders of five ponds within the town of Plymouth. Unlike the previous few years when shorelines of these groundwater ponds were well up into the shrub fringe, a return to a more normal precipitation in 1974–75 produced moist exposed shelves varying in width from less than five feet to, in extreme cases, over fifty feet. The change in the plant life inhabiting these strands was profound. This year in Plymouth such species as *Sagittaria teres* S. Watson, *Rhynchospora macrostachya* Torr., and *Lycopus amplectens* Raf. were widely distributed and common; numerous stations were found for *Scleria reticularis* Michx., *Drosera filiformis* Raf., and *Utricularia cornuta* Michx.; and several ponds

[1]Research Report No. 9 of the Manomet Bird Observatory, Manomet, Mass. 02345.

supported stands of these New England rarities: *Eleocharis tuberculosa* (Michx.) R. & S., *Psilocarya scirpoides* Torr., *Fuirena squarrosa* Michx. var. *pumila* Torr., *Utricularia resupinata* B. D. Greene, and *Eupatorium leucolepis* (DC.) T. & G. var. *novae-angliae* Fern.

On 26 August 1975 while botanizing at Kings Pond in western Plymouth, a low-growing sedge of the pond margin attracted my attention. Closer inspection revealed that two species were present. The first, occupying the wetter, muddy-peaty sites, and with rufous-brown spikelets proved to be *Psilocarya scirpoides;* the other, occupying somewhat drier, sandy-peaty sites, and with gray-brown spikelets was *P. nitens.* Thus 50 years had passed between the first and second reports of this rare sedge. Interestingly, the difference noted in microhabitat preference was found to hold true in subsequent localities where either or both species were present, although *P. scirpoides* was occasionally found in moist sand.

The following is a summary of known stations for *Psilocarya nitens* in New England; all are in Plymouth, Massachusetts. 1. Kings Pond, uncommon on northwest and northeast shores. 2. Big West Pond, uncommon on eastern shore. 3. Little Micajah Pond, two plants found on northwest shore. 4. West Spectacle Pond (west of Little Micajah Pond), frequent on eastern shore. 5. Grassy Pond (south of Bloody Pond), two plants found on the peninsula.

Collections of *Psilocarya nitens* have been deposited in the herbaria of Harvard University (GH), University of Massachusetts at Amherst (MASS), and the New England Botanical Club (NEBC).

POINT REYES BIRD OBSERVATORY
4990 STAR ROUTE
STINSON BEACH, CALIF. 94970

RUDBECKIA SEROTINA F. TUBULIFORMIS IN NEW ENGLAND

The herbarium specimen of *Rudbeckia serotina* Nutt., on the basis of which this note has been written, was collected by me on July 27, 1975, near the town of Northfield, Orange Co., Vermont. In the field, the plants attracted my attention by the abnormal, tubular, ray flowers in their heads.

In the corrected, eighth edition of *Gray's Manual of Botany* (3), on page 1485, several monstrous forms of *Rudbeckia serotina* are listed. The specimen under discussion matches well with the description of forma *tubuliformis* (Burnh.) Fern. & Schub.: "ligules orange-yellow, tubular at least below."

Forma *tubuliformis* (Burnh.) Fern. & Schub. of *Rudbeckia serotina* Nutt. was originally described by S. H. Burnham in 1914 as a variety of *Rudbeckia hirta* L. (1). In 1948, M. L. Fernald and B. G. Schubert transferred this variety to *Rudbeckia serotina* Nutt. and changed its status to the rank of form (2).

In F. C. Seymour's *The Flora of New England* (4), this form is not listed, and I could not find it in the herbarium collections of the New England Botanical Club. Consequently, it might be that this is the first record of this form in New England. In view of this possibility, I am reporting this collection. For the same reason, I deposited a voucher specimen of *Rudbeckia serotina* Nutt. f. *tubuliformis* (Burnh.) Fern & Schub. from the above cited locality in the herbarium ot the New England Botanical Club.

I am grateful to the Gray Herbarium — Arnold Arboretum Library for access to the necessary literature, and to the New England Botanical Club for access to its herbarium, which was helpful for preparation of this note.

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A. I. BARANOV
14 EGMONT ST. APT. 6
BROOKLINE, MASSACHUSETTS 02146

RED FORM OF LINDERA BENZOIN

A form of *Lindera benzoin* (L.) Blume, which deviates from the normal yellow-flowered shrub only in the production of brick-red flowers, is here reported. The one shrub seen was staminate, and no fruit is available for comparison with the typical form, nor does the fall coloring of the leaves differ in any way from the usual yellow. The winter buds, however, are easily distinguished from the typical in their darker, red-brown coloring.

The specimen observed occurs at Hopkinton, Washington County, Rhode Island, on the Woodville Road, and was first noticed on April 25, 1974, when it was in flower. In May, 1975, cuttings were sent to the Arnold Arboretum, at their request, for propagation. The following name for this red-flowered plant is proposed.

Lindera benzoin (L.) Blume forma **rubra** R. L Champlin, forma nova.

A typica differt floribus staminatis rubris. TYPE: **Rhode Island.** WASHINGTON COUNTY: low woods, Hopkinton. *R. L. Champlin s.n.* (Holotype, NEBC).

RICHARD L. CHAMPLIN
PRISCILLA ROAD
JAMESTOWN, RHODE ISLAND 02835

NOTICE OF PUBLICATION

The Concord Field Station of Harvard University has recently published a thirty-nine page ". . . informal but comprehensive guide for the identification of all trees growing wild in Concord, Massachusetts and neighboring townships." The contents of *Concord Area Trees* include species descriptions, black and white illustrations, a glossary, bibliography, fruit index, and a general index. Copies of this guide may be obtained for $1.50 each by writing the Concord Field Station, Harvard University, Old Causeway Road, Bedford, MA 01730.

Rhodora

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BIOSYSTEMATICS OF PSILOSTROPHE DC. (COMPOSITAE) I. CHROMOSOME VARIABILITY[1]

ROY CURTISS BROWN

The genus *Psilostrophe* DC. (Compositae:Helenieae) consists of seven species of conspicuous, weedy herbs commonly referred to as paperflowers, which are common and showy elements of the summer flora in the semiarid regions of the southwestern United States and adjacent Mexico. The species are closely related and most taxonomic difficulties apparent in the genus arise from the substantial morphologicai similarities of the species. It was conceivable that a study of chromosome numbers and meiotic behavior in wild plants and studies of experimentally synthesized hybrids might help to clarify the evolutionary relationships and status of the taxa. The purpose of this paper is to summarize information on chromosome numbers in the genus and present evidence of structural hybridity and numerical variation in some species.

MATERIALS AND METHODS

Meiosis was studied in cells undergoing microsporogenesis. For this purpose young capitula collected in the field or greenhouse were fixed in a modified Carnoy's solution of chloroform: 95% ethanol: glacial acetic acid (4:3:1 V/V/V) and placed under refrigeration as quickly as possible. After a period of 24 to 48

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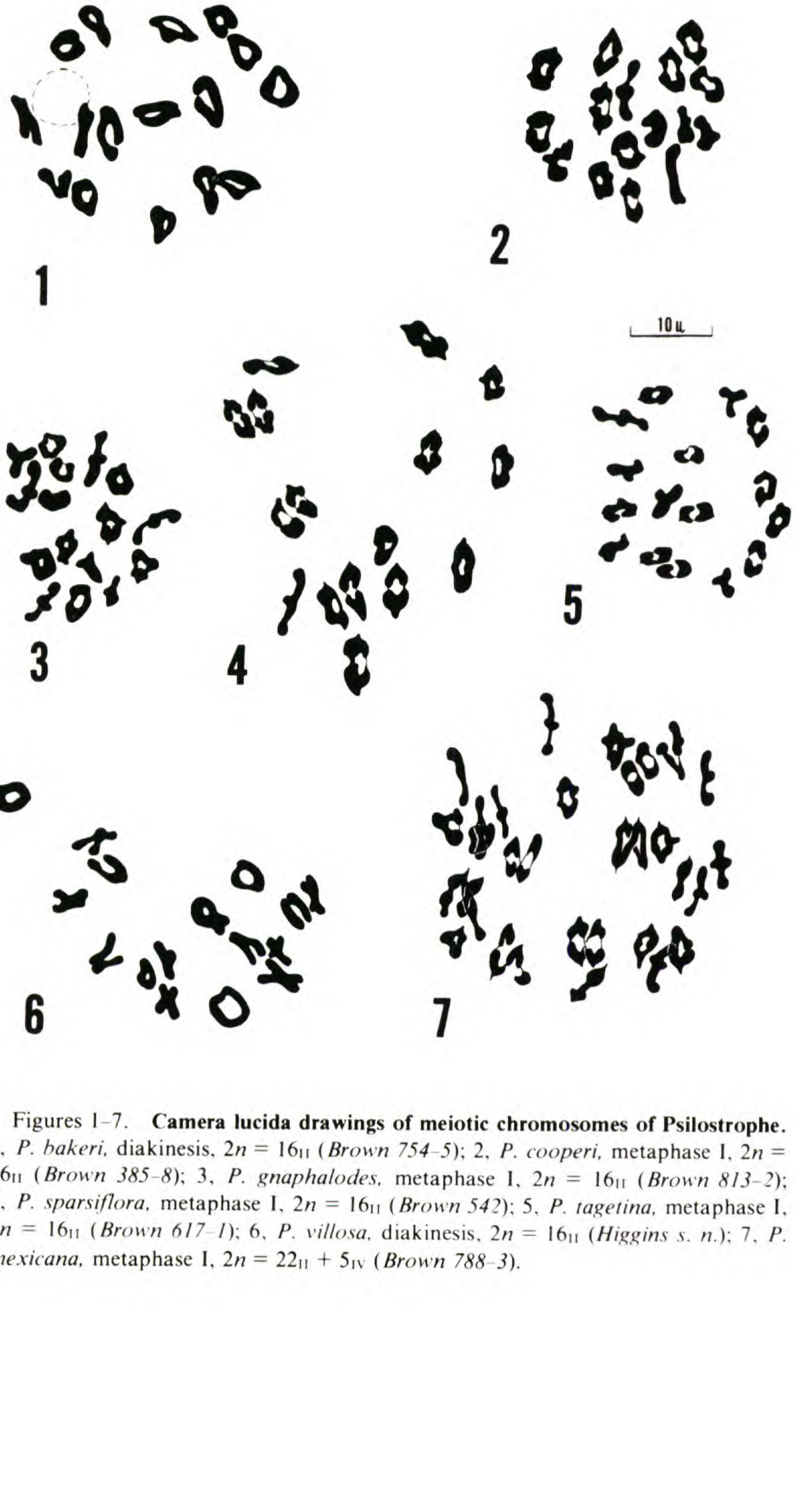
[1]I thank Donald J. Pinkava for his guidance in this study, which formed part of a thesis submitted in partial fulfillment of the requirements of the Ph.D. degree at Arizona State University, Tempe. I also gratefully acknowledge Harlan Lewis for his review of this paper.



Figures 1–7. **Camera lucida drawings of meiotic chromosomes of Psilostrophe.** 1, *P. bakeri*, diakinesis, $2n = 16_{II}$ (*Brown 754–5*); 2, *P. cooperi*, metaphase I, $2n = 16_{II}$ (*Brown 385–8*); 3, *P. gnaphalodes*, metaphase I, $2n = 16_{II}$ (*Brown 813–2*); 4, *P. sparsiflora*, metaphase I, $2n = 16_{II}$ (*Brown 542*); 5, *P. tagetina*, metaphase I, $2n = 16_{II}$ (*Brown 617–1*); 6, *P. villosa*, diakinesis, $2n = 16_{II}$ (*Higgins s. n.*); 7, *P. mexicana*, metaphase I, $2n = 22_{II} + 5_{IV}$ (*Brown 788–3*).

hours, the fixed material was transferred to 70% ethanol and stored under refrigeration. Entire florets were stained in aceto-carmine. The stained anthers were teased free from the floret and squashed in a drop of Hoyer's solution yielding a semi-permanent preparation (Beeks, 1955). Mitotic metaphase chromosomes were studied in root tip cells. Following a pretreatment in 1% colchicine for four hours, root tips were similarly fixed and stored. After softening in a solution of HCl: 95% ethanol (1:1 V/V) for three minutes, the root tips were stained with aceto-carmine and squashed in Hoyer's solution. Voucher specimens are deposited in the Arizona State University Herbarium (ASU); duplicates to be distributed.

RESULTS

The base chromosome number (x) in *Psilostrophe* is 16 (Tables 1 & 3). Observations of somatic chromosomes show a symmetrical karyotype of uniform chromosomes all of a similar length and possessing a median to submedian centromere (Figure 8). The diploid species investigated possess one pair of satellite chromosomes; otherwise, individual chromosomes could not be distinguished.

The counts reported in Table 1 indicate that polyploidy is rare in the genus, manifest only in the tetraploid, *Psilostrophe mexicana,* but chromosome variability within populations is common in several diploid species. These chromosomal differences occur as both structural rearrangements and as differences in the presence and number of supernumerary (B) chromosomes.

Structural hybridity. The principal chromosome rearrangements detected were reciprocal translocations which were found in naturally occurring populations of five of the six diploid species (Table 3 & Figures 9–14). Plants heterozygous for one or occasionally two reciprocal translocations are recognizable by the formation of one or two rings of four chromosomes in metaphase I. Plants which have such ring configurations occasionally exhibit a chain of four chromosomes due probably to the failure of chiasmata formation in one arm (Figures 12 & 13). Only *Psilostrophe sparsiflora* of the diploid species is found thus far to be free from translocation heterozygosity, and it is limited in distribution to a relatively small geographical region in southern

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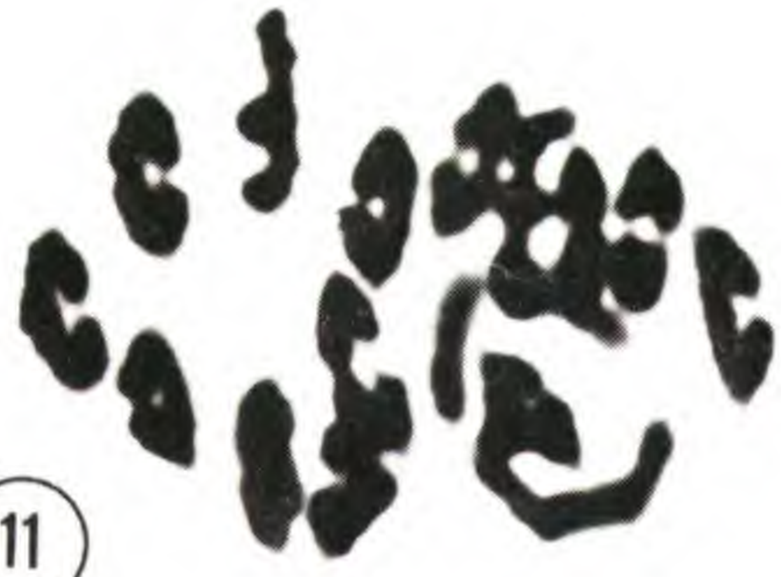

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Utah and northern Arizona where it does not appear to be actively evolving as evidenced by the uniform morphology of different populations. However, only a few populations have been examined cytogenetically and additional study may well establish the presence of translocation heterozygosity in this species. As may be seen in Table 3, over a third of the populations studied in each of the five remaining diploid species contained at least one plant heterozygous for a single translocation. Although numerous multivalent configurations were observed in the tetraploid *P. mexicana,* they are not considered here because of the inherent difficulties in distinguishing tetravalents due to duplications of chromosomes from tetravalents due to translocation heterozygosity.

Only a relatively few individuals from each population were examined cytogenetically in this initial survey. Thus, while plants heterozygous for one or more translocations are known to be geographically widespread, very little is known of the frequency of translocation heterozygosity within populations, although the frequency with which they have been found suggests it is quite high. Two distinct populations of *Psilostrophe tagetina* from the foothills of the Chiricahua Mountains in southeastern Arizona were examined in greater detail than the rest. Of the twelve plants examined from a population located near Paradise on the eastern slopes of the Chiricahuas, three (25%) were found to be heterozygous for a single translocation. The other population examined is located in the western foothills near the historical site of Fort Bowie. Eight plants from this population were examined cytologically; six (75%) were heterozygous for one or more translocations. Two interchanges occurred in one plant which consistently possessed a meiotic configuration of $12_{II}+2_{IV}+1B_{I}$

Figure 8. **Mitotic chromosomes of Psilostrophe tagetina.** $2n = 32 + 1B$ (arrow); cell from squash of colchicine treated root tip. × 1200.

Figures 9–14. **Translocation heterozygosity in species of Psilostrophe.** All × 1200. 9, *P. bakeri,* photomicrograph, metaphase I, $2n = 14_{II}+1_{IV}$ (*Brown 764*); 10, *P. cooperi,* camera lucida drawing, metaphase I, $2n = 12_{II}+2_{IV}$ (*Brown 622–1*); 11, *P. gnaphalodes,* photomicrograph, metaphase I, $2n = 14_{II}+1_{IV}$ (*Keil 7895*); 12, *P. tagetina,* photomicrograph, metaphase I, $2n = 12_{II}+2_{IV}$ (rings) + $1B_{I}$ (*Brown 399*); 13, same as 12 but with one ring quadrivalent and one chain quadrivalent; 14, *P. villosa,* camera lucida drawing, metaphase I $2n = 14_{II}+1_{IV}$ (*Higgins s. n.*).

Table 1. **Meiotic Configurations in Natural Populations of Psilostrophe.**

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe bakeri (A. Gray) Greene	**United States:** COLORADO: Delta Co.: 14.2 mi NW of Delta along Hwy 50, *Brown 759–2 & 759–3.*	$16_{II}(2)$*
	United States: COLORADO: Delta Co.: Tongue Creek Orchards NW of Orchard City, *Brown 764.*	$14_{II}+1_{IV}(1)$
	United States: COLORADO: Mesa Co.: W of Grand Junction, *Brown 754–1 & 754–5.*	$16_{II}(2)$
Psilostrophe cooperi (A. Gray) Greene	**United States:** ARIZONA: Graham Co.: Cemetery ridge overlooking Solomon, *Brown 401–2.*	$16_{II}(1)$
	United States: ARIZONA: Maricopa Co.: 14 mi S of Aquila along Eagle Eye Road, *Lehto 3578.*	$16_{II}(1)$
	United States: ARIZONA: Maricopa Co.: Cave Creek, *Brown 385–8.*	$16_{II}(1)$
	United States: ARIZONA: Mohave Co.: .25 mi E of Burro Creek, *McLeod 453 & 452.*	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	United States: ARIZONA: Pima Co.: Organ Pipe National Monument, *Pinkava 10035.*	$14_{II}+1_{IV}(1)$
	United States: ARIZONA Pima Co.: 4.1 mi SSW of Redington along road to Tanque Verde, *Pinkava 10942 & 10941.*	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	United States: ARIZONA: Santa Cruz Co.: N of Elgin along Hwy 83, *Brown 622–1.*	$12_{II}+2_{IV}(1)$
	United States: ARIZONA: Yuma Co.: 13 mi N of Wenden. *Pinkava 10354.*	$16_{II}(1)$

Table 1 (Continued).

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe gnaphalodes DC.	**Mexico:** COAHUILA: 11.3 mi S of Rio Salada along Hwy 57, *Keil 7874B.*	$16_{II}(1)$
	Mexico: COAHUILA: ca. 63 mi S of Monclova along Hwy 57, *Pinkava 10529 & 10530.*	$16_{II}(2)$
	Mexico: COAHUILA: 50 mi S of Piedras Negras; 1.6 mi N of El Infante along Hwy 57, *Keil 7840.*	$14_{II}+1_{IV}(1)$
	Mexico: COAHUILA: 23 mi W of Paila along Hwy 40, *Keil 7965*[a]	$16_{II}(1)$; $14_{II}+1_{IV}(1)$
	Mexico: COAHUILA: 5.3 mi E of Paila along Hwy 40, *Keil 7955 & 7955*[a].	$16_{II}(1)$; $12_{II}+2_{IV}(1)$
	Mexico: COAHUILA: 1.5–6.5 mi E of General Cepeda along Hwy 40, *Brown 813–2 & 814–1.*	$16_{II}(1)$; $12_{II}+2_{IV}(1)$
	Mexico: COAHUILA: Muralla Pass 46.2 mi S of Monclova, *Keil 7895.*	$14_{II}+1_{IV}(1)$
	Mexico: NUEVO LEON: 6.7 mi E of San Roberto along road to Linares, *Pinkava 10550.*	$16_{II}(1)$
	United States: TEXAS: Brewster Co.: 1.2 mi N of Persimmon Gap Ranger Station, *Keil 7830.*	$14_{II}+1_{IV}(1)$
Psilostrophe mexicana R. C. Brown	**Mexico:** CHIHUAHUA: 7–8 mi N of junction to Jiménez along Hwy 45, *Brown 788–1, 788–3 & 789–1.*	$18_{II}+7_{IV}(1)$; $22_{II}+5_{IV}(2)$
	Mexico: CHIHUAHUA: Between Parral and Jiménez 2.6 mi W of Hwy 49, *Keil 8238.*	$22_{II}+5_{IV}(1)$
	Mexico: DURANGO: La Resolana, *Brown 800.*	$24_{II}+4_{IV}(1)$
	Mexico: DURANGO: 2.7 mi S of La Zarca along Hwy 45, *Brown 803–1 & 803–4.*	$22_{II}+5_{IV}(1)$; $14_{II}+9_{IV}(1)$

Table 1 (Continued)

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe sparsiflora (A. Gray) A. Nels.	**United States:** ARIZONA: Coconino Co.: Meteor Crater, *Brown 493 & 536.*	$16_{II}(2)$
	United States: ARIZONA: Coconino Co.: 5 mi NW of Wupatki Natl. Monument, *Brown 542.*	$16_{II}(1)$
	United States: ARIZONA: Coconino Co.: N of Sunset Crater at Natl. Forest boundary, *Brown 420.*	$16_{II}(1)$
	United States: ARIZONA: Mohave Co.: 2 mi W of Peach Springs on Hwy 66 then .4 mi N along Buck and Doe Road, *McLeod 1011.*	$16_{II}(1)$
Psilostrophe tagetina (Nutt.) Greene	**Mexico:** CHIHUAHUA: 8.7 mi W of Hwy 45 along Hwy 2, *Keil 8448 & 8448*[a].	$14_{II}+1_{IV}1B_{I}(2)$
	Mexico: CHIHUAHUA: 8.4 mi S of Nuevo Casas Grandes, *Keil 8396.*	$16_{II}(1)$
	United States: ARIZONA: Apache Co.: 1.2 mi E of Hwys 180 and 666 along Hwy 60, *Brown 617-1 & 617-2.*	$16_{II}(1)$; $16_{II}+3B_{I}(1)$
	United States: ARIZONA: Cochise Co.: Chiricahua Mtns.; junction of Portal Road and road to Paradise, *Brown 819-1.*	$16_{II}(1)$
	United States: ARIZONA: Cochise Co.: Paradise, *Brown 398, 821-1-11.*	$16_{II}(2)$; $14_{II}+1_{IV}(1)$; $14_{II}+1_{IV}+1B_{I}(1)$; $16_{II}+1B_{I}(3)$; $16_{II}+1B_{II}(1)$; $16_{II}+2B_{II}(1)$
	United States: ARIZONA: Cochise Co.: 5.3 mi S of Fort Bowie turnoff along Hwy 186, *Brown 399, 601, 604-608.*	$16_{II}(3)$; $14_{II}+1_{IV}(4)$; $12_{II}+2_{IV}+1B_{I}(1)$
	United States: ARIZONA: Cochise Co.: Apache Pass, W of the summit, *Brown 825-2 & 825-3.*	$16_{II}+1B_{I}(1)$; $12_{II}+2_{IV}(1)$

Table 1 (Continued)

Taxon	Population & Voucher	Meiotic Configuration
Psilostrophe tagetina (Nutt.) Greene (Continued)	**United States:** NEW MEXICO: Grant Co.: .3 mi S of Hwy 61 along Hwy 180, *Keil 8461A*.	$16_{II}+1B_{I}(1)$
	United States: NEW MEXICO: Santa Fe Co.: 7.3 mi N of Stanley along Hwy 41, *Keil 7648*.	$16_{II}(1)$
	United States: NEW MEXICO: Torrance Co.: 10 mi E of Mountainair, *Keil 7652*.	$16_{II}(1)$
	United States: TEXAS: Brewster Co.: Big Bend National Park: 15.1 mi N of Castolon, *Keil 7802A & 7802*[a].	$16_{II}(2)$
	United States: TEXAS: Brewster Co.: 13 mi E of entrance to Big Bend National Park, *Keil 7792*.	$14_{II}+1_{IV}(1)$
	United States: TEXAS: Jeff Davis Co.: Davis Mtns., *Keil 7701 & 7701*[a].	$16_{II}(1)$; $16_{II}+1B_{I}(1)$
Psilostrophe villosa Rydb.	**United States:** TEXAS: Randall Co.: ca. 1 mi NW of Canyon, *Higgins s. n. & s. n.*[a].	$16_{II}(1)$; $14_{II}+1_{IV}(1)$

*Number in parentheses denotes the number of plants examined.
[a]Cultivated from wild achenes.

(Figures 12 & 13), the maximum number of translocations detected in any one plant. One other plant from a nearby, but distinct, population also possessed two rings of four chromosomes but lacked the supernumerary chromosome.

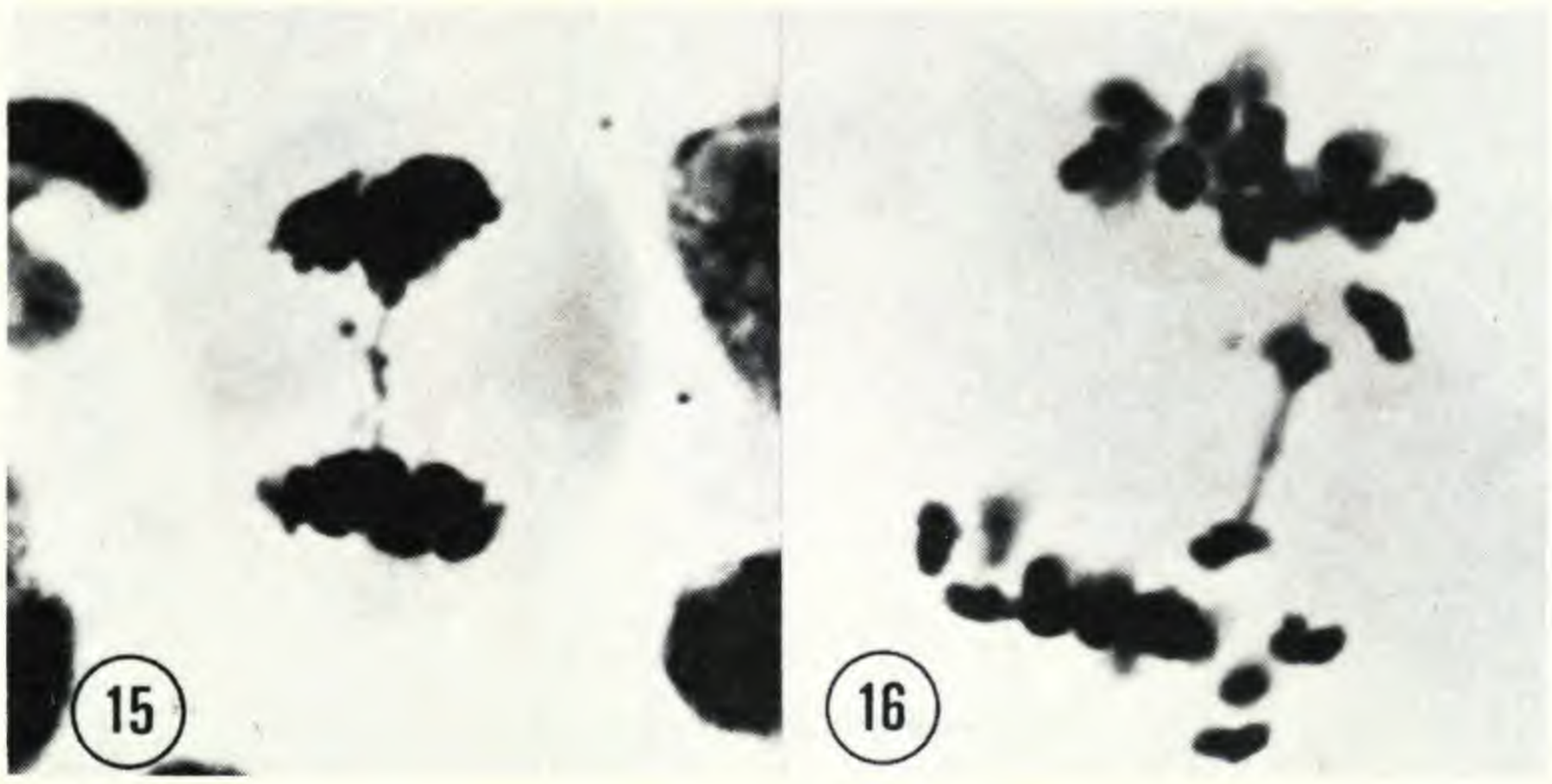
The ring of four configuration in *Psilostrophe* appears regularly to undergo an alternate segregation. Thus, the presence of interchange heterozygosity does not appear to lower the fertility appreciably. Pollen stainability in lactophenol-cotton blue (Maneval, 1936) is a high 92–99% in *P. tagetina* heterozygotes.

Plants heterozygous for inversions detectable by a bridge and fragment configuration are apparently much rarer than translocation heterozygotes in the genus, although "false-bridging" caused by stickiness of the chromosomes in anaphase I was particularly troublesome in this study. False bridges are fairly common in other genera of the Compositae and apparently do not adversely affect meiosis (Pinkava, 1964). Persistent anaphase I bridges plus an acentric fragment were observed in an individual of *Psilostrophe tagetina* (Figure 15) and one plant of *P. gnaphalodes* (Figure 16). Such inversions frequently occur in natural populations of flowering plants where they are, in most cases, only transitory and adaptively neutral unless they are associated with gene combinations of selective value (Stebbins, 1950). The role of inversion in the evolution of *Psilostrophe* is not known, but probably has had little effect for none of the artificial interspecific hybrids examined showed any evidence of inversion heterozygosity.

Chromosome configurations in experimental hybrids. Cytogenetic analysis of hybrids reveals a high degree of homology in chromosome structure among the species (Table 2 & Figures 17–23). In no case does the degree of heterozygosity for translocations in the hybrids exceed that present in the parental plants. The lack of evidence of meiotic abnormalities such as bridges, fragments or univalents makes it unlikely that the genomes of the species have been extensively rearranged.

Supernumerary chromosomes. From one to four supernumerary or B chromosomes frequently occur in natural populations of *Psilostrophe tagetina* (Table 3). While B chromosomes have not yet been detected in any of the remaining diploid species, their presence is to be expected in *P. gnaphalodes* and *P. villosa* for these two species are genetically closely related to *P. tagetina* (Brown, 1974b). An individual of *P. villosa* possessing 17 pairs of chromosomes has been reported (Powell & Turner, 1963) and 18 pairs plus 2 fragments has been reported in *P. tagetina* (Powell & Sikes, 1970). My study of *P. tagetina* suggests that these examples of extra bivalents probably represent paired supernumerary chromosomes.

The occurrence of supernumerary chromosomes in *Psilostrophe tagetina* seems to be correlated with populations containing translocation heterozygotes as has also been reported in other



Figures 15 & 16. **Persistent anaphase I bridge and fragment configurations.** All × 1200. 15, *Psilostrophe tagetina* (*Keil 8461*); 16, *P. gnaphalodes* (*Keil 7955*).

groups of plants, e. g. *Clarkia* (Lewis, 1951 & 1968). Six of the twelve populations of *P. tagetina* examined contained individuals with B chromosomes and three of these populations also contain plants heterozygous for one or more translocations (Figure 24). I feel confident that when an adequate number of plants are sampled from additional populations an even stronger coincidence of B chromosomes and translocation heterozygosity will be found.

The supernumerary chromosomes apparently are stable in meiosis as indicated by the lack of chromosome lagging and subsequent micronucleus formation at the dyad or tetrad stages of meiosis. The occurrence of such micronuclei (Figure 25), although rare, does provide evidence of a mechanism for reducing the number of B chromosomes in the gametes. When only one supernumerary was present it could be detected as a univalent in prophase I through metaphase I (Figure 26). The supernumerary chromosomes showed no tendency to pair with any member of the regular complement. Anaphase I stages were rarely observed in *Psilostrophe tagetina;* the few that were adequate for analysis indicated that, in plants with one supernumerary, the supernumerary regularly undergoes a reductional division at anaphase I giving a 16–17 separation (Figure 27).

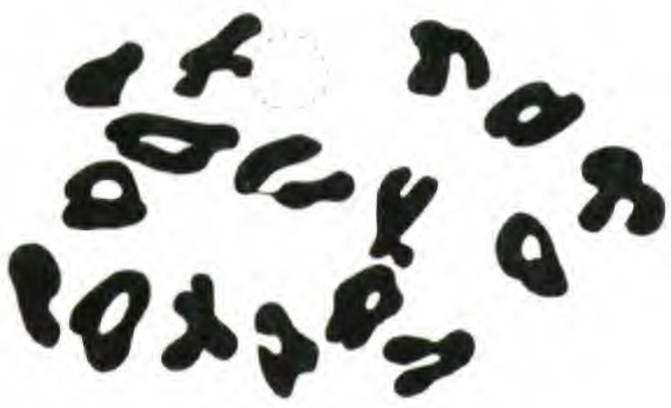

17


18


19


20


21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23

Figures 17–23. **Camera lucida drawings of meiotic chromosomes of experimental hybrids in Psilostrophe.** 17, *P. tagetina* × *P. gnaphalodes*, metaphase I, $2n = 16_{II}$; 18, *P. tagetina* × *P. villosa*, metaphase I, $2n = 14_{II}+1_{IV}$; 19, *P. sparsiflora* × *P. tagetina*, metaphase I, $2n = 14_{II}+1_{IV}$; 20, *P. sparsiflora* × *P. tagetina*, diakinesis, $2n = 16_{II}+1B_I$; 21, *P. sparsiflora* × *P. gnaphalodes*, metaphase I, $2n = 16_{II}$; 22, *P. cooperi* × *P. gnaphalodes*, diakinesis, $2n = 16_{II}$; 23, *P. cooperi* × *P. sparsiflora*, diakinesis, $2n = 14_{II}+1_{IV}$.

When two or more supernumerary chromosomes are present in a plant there is a marked tendency for them to pair in prophase I giving rise to bivalents which are decidedly smaller than the regular bivalents. An individual collected near Eager, Apache County, Arizona, was found to possess 16 regular bivalents plus 3 B chromosomes at metaphase I. In some microsporocytes the three supernumerary chromosomes formed a bivalent plus a univalent in prophase I (Figure 29); in others, the three supernumerary chromosomes occurred as univalents (Figure 28). No cases were observed in which the B chromosomes existed as a trivalent. Another plant from the eastern foothills of the Chiricahuas possessed 4 supernumerary chromosomes in addition to the A complement of 16 pairs. The majority of the microsporocytes examined in this plant showed the B chromosomes to exist as one pair and two univalents in prophase I. However, in some cells the supernumeraries occurred as two pairs of chromosomes which appeared to be joined by a single chiasma at diakinesis. The two supernumerary pairs are easily distinguished from the doughnut-like bivalents of the A complement by their smaller size and rod-like shape (Figure 30). The paired supernumerary chromosomes apparently separate regularly in anaphase I.

Polyploidy. The discovery of polyploidy in *Psilostrophe* has led to the recognition of a new species, *P. mexicana* (Brown, 1974a), with $2n = 64$. Tetraploidy was first noticed in the genus by De Jong and Longpre (1963) who reported an individual of *P. gnaphalodes* possessing 32 pairs of chromosomes. All subsequent counts show the tetraploids to possess from one to nine multivalents (Table 1), mostly as rings or chains of four chromosomes (Figure 7). Meiosis is regular for the most part although some lagging and persisting anaphase I bridges were observed. The evolutionary origin of this tetraploid taxon has not yet been studied experimentally. However, *P. mexicana* is morphologically and geographically most closely related to *P. gnaphalodes* and *P. tagetina* of the existing diploid species. I would point out that the existence of tetravalents in *P. mexicana* does not necessarily indicate origin by autotetraploidy, for the genomes of the aforementioned diploid species are closely related and artificial hybrids between them almost always show 16 bivalents in meiosis (Table 2 & Figure 17). Thus, the allopolyploid derivatives of such hybrids conceivably could possess several multivalents.

Table 2. **Chromosome Configurations in Experimental Hybrids of Psilostrophe.**

Cross & Meiotic Configurations[a]	Hybrid Configuration
INTRASPECIFIC CROSSES	
P. tagetina ($14_{II}+1_{IV}$) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	16_{II}
Reciprocal	$14_{II}+1_{IV}$
P. tagetina (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$14_{II}+1_{IV}+1B_I$
INTERSPECIFIC CROSSES	
P. tagetina (16_{II}) × **P. gnaphalodes** ($14_{II}+1_{IV}$)	16_{II} (Figure 17)
Reciprocal	16_{II}
P. tagetina ($14_{II}+1_{IV}$) × **P. villosa** ($14_{II}+1_{IV}$)	$14_{II}+1_{IV}$ (Figure 18)
P. sparsiflora (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$14_{II}+1_{IV}$ (Figure 19)
P. sparsiflora (16_{II}) × **P. tagetina** ($12_{II}+2_{IV}+1B_I$)	$16_{II}+1B_I$ (Figure 20)
P. sparsiflora (16_{II}) × **P. gnaphalodes** (16_{II})	16_{II} (Figure 21)
P. cooperi ($14_{II}+1_{IV}$) × **P. gnaphalodes** ($14_{II}+1_{IV}$)	16_{II} (Figure 22)
P. cooperi (Undetermined) × **P. sparsiflora** (16_{II})	$14_{II}+1_{IV}$ (Figure 23)

[a]Ovulate parent listed first.

DISCUSSION

Individuals heterozygous for one or two reciprocal translocations frequently occur in populations of the diploid *Psilostrophe* species. The occasional occurrence of plants heterozygous for a translocation has been reported for a wide variety of flowering plants (for a review see Burnham, 1956). In the vast majority of cases the translocations are transitory and of minor evolutionary significance. It seems unlikely that the common and geographically widespread occurrence of translocation heterozygosity in the diploid species of *Psilostrophe* is due to chance alone. It is more probable that the chromosome structural hybridity is part of the adaptive genetic complex in these populations.

The high frequency of translocation heterozygosity found in *Psilostrophe* may have one of two explanations. The translocation heterozygotes may have an adaptive superiority to either of the two possible homozygous conditions, or the chromosomally polymorphic populations may be the result of recent hybridization between populations differing by a translocation. That the chromosomally polymorphic populations may be the result of

recent hybridization seems highly improbable. Translocation heterozygosity has been observed in five of the six diploid species and often in widely disjunct populations. Also important is the finding that interpopulational F_1 hybrids show no greater degree of translocation heterozygosity than intrapopulational experimental hybrids. It is reasonable to assume, therefore, that the widespread occurrence of translocation heterozygosity in the diploid species of *Psilostrophe* is due to the superior fitness of the heterozygotes themselves. However, as pointed out by John and Lewis (1966), while the theory of superior fitness of the heterozygote has often been put forth to explain systems of chromosome structure polymorphism, experimental proofs of the supposed heterozygous advantage are very few. An exceptional case for the existence of chromosome structure heterosis is found in *Drosophila* where certain polymorphisms (for inversions) are maintained chiefly by the superior fitness of the structural heterozygotes to either of the homozygous conditions when fitness is measured in terms of ability to metabolize nutrient media (Dobzhansky, 1961).

Translocation heterozygosity in *Campanula* has been demonstrated to function in maintaining genetic heterozygosity in the face of forced inbreeding by Darlington and LaCour (1950). In this example the greater the frequency of inbreeding, the greater was the selection for interchange heterozygotes. By analogy with this situation, translocation heterozygosity is believed to have similar effects in *Isotoma petraea* (Lobeliaceae) (James, 1965) and *Clarkia williamsonii* (Onagraceae) (Wedberg, Lewis, & Venkatesh, 1968).

In predominantly outbreeding plants such as *Psilostrophe*, translocations, like other structural rearrangements, may be important in restricting recombinational events. Translocations may allow the transmission of a favorable combination of genes as a block without the necessity of bringing the co-adapted genes together on the same chromosome (Stebbins, 1950). Of the three anaphase I disjunction patterns possible in a ring-of-four chromosomes, only the alternate pattern results in a balanced complement which is free from duplications or deficiencies, barring the very rare occurrence of cross-overs in the interstitial regions. In this manner recombination within a translocation is curtailed and a favorable linkage group maintained.

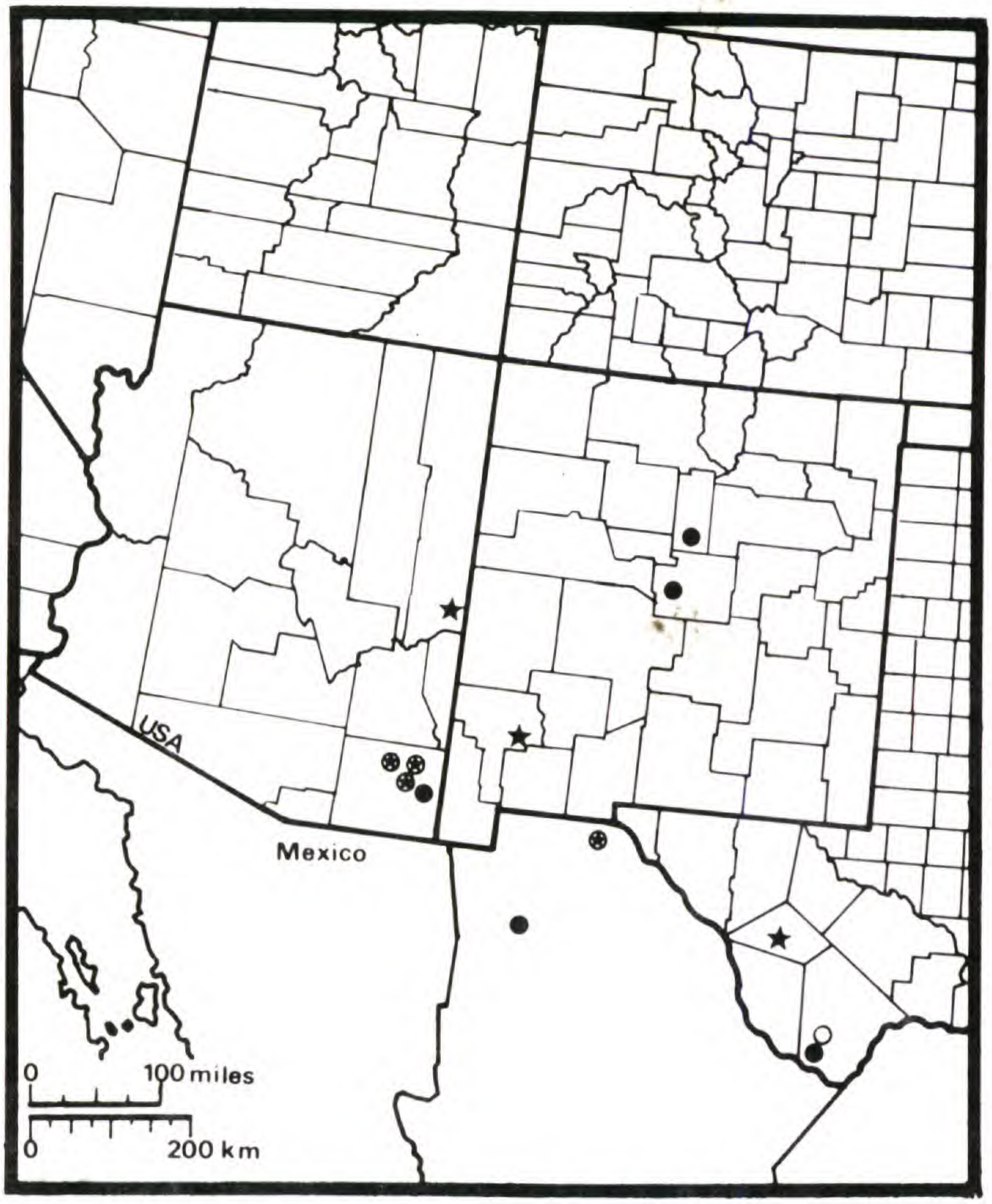
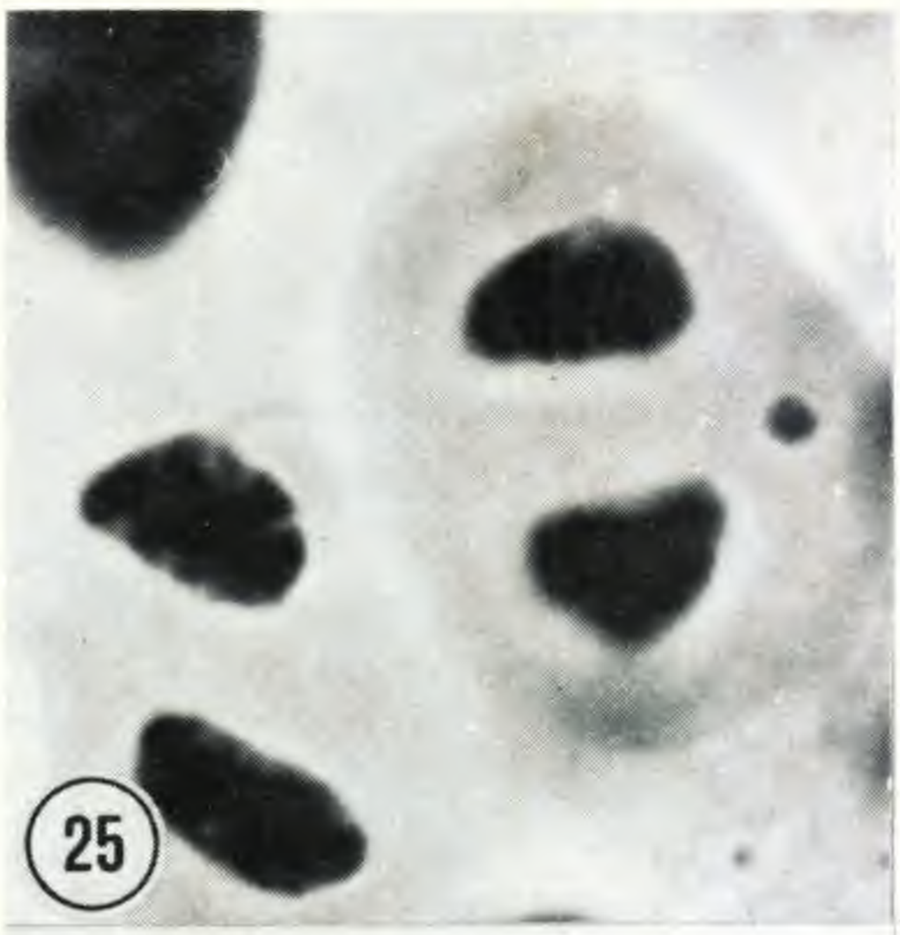
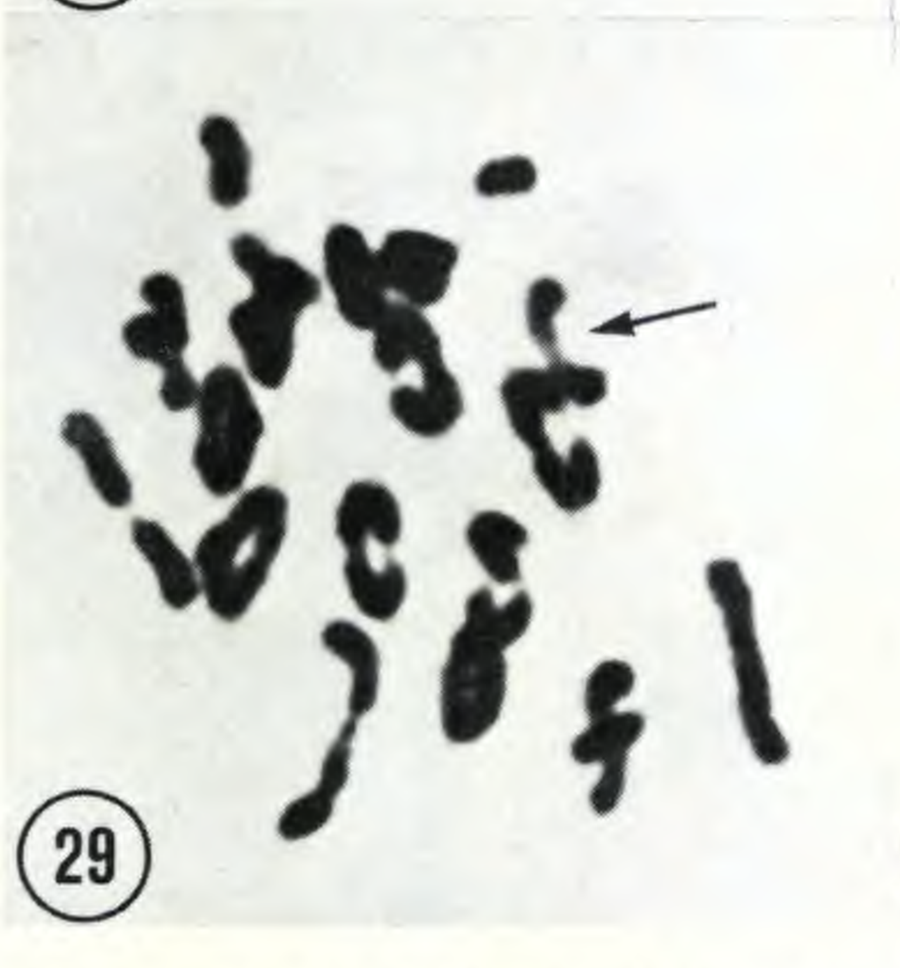


Figure 24. **Known distribution of supernumerary chromosomes and interchange heterozygotes in Psilostrophe tagetina.** Homozygous populations are represented by black dots; homozygous + B chromosomes are represented by black stars. Heterozygous populations are represented by white dots; heterozygous + B chromosomes are represented by circled stars.

Interchromosomal linkage can be realized only if interchange heterozygotes are not associated with a marked lowering of the fertility. The strong tendency of the ring-of-four chromosomes in *Psilostrophe* to undergo an alternate segregation in anaphase I results in the majority of the gametes with a balanced complement of genes. Thus, the presence of interchange heterozygosity in *Psilostrophe* does not result in a substantially lowered fertility when pollen stainability in lactophenol-cotton blue is used as an indicator of fertility. Such a non-random anaphase I disjunction pattern is known in other genera, e. g. *Oenothera* (Cleland, 1936)





Figures 25–30. **Meiotic behavior of supernumerary** (B) **chromosomes in Psilostrophe tagetina.** Figure 27 is a camera lucida drawing; all others are photomicrographs. Arrows indicate paired supernumerary chromosomes. All × 1200. 25, Dyad with micronucleus; 26, metaphase I, $2n = 16_{II}+1B_I$; 27, 16–17 segregation in anaphase I; 28, metaphase I, $2n = 16_{II}+3B_I$; 29, metaphase I, $2n = 16_{II}+1B_{II}+1B_I$; 30, diakinesis, $2n = 16_{II}+2B_{II}$.

and *Clarkia* (Lewis, 1953). Such plants are said to have a directed segregation (Burnham, 1956). According to Burnham, a directed segregation is dependent upon a karyotype with chromosomes of a uniform size with median to submedian centromeres. *Psilostrophe* is seen to possess such a karyotype, and in this respect, the structural hybridity is not unlike the well studied situations in *Paeonia* (Walters, 1942), *Clarkia* (Lewis, 1953), and *Oenothera* (Cleland, 1962). The development of a directed segregation also demands that chiasmata formation be confined to the ends of the chromosomes or terminalize very rapidly allowing sufficient flexibility for the ring to assume the "figure eight" configuration necessary in alternate segregation. Studies of chiasmata formation in *Psilostrophe* have not progressed sufficiently to say this is the case.

Interestingly, structural rearrangement of the chromosomes does not appear to have been a major force in the speciation of *Psilostrophe*. Analysis of interspecific hybrids failed to detect any individuals which possessed a greater degree of translocation heterozygosity than their respective parental taxa. Bivalents are the general rule in the experimental interspecific hybrids indicating that the genomes of the species have not been extensively rearranged. Often a translocation heterozygote of one species when crossed with a homozygote of another species yielded F_1 plants with 16 bivalents in meiosis. A similar situation is known in *Camissonia* (Onagraceae) in which hybrids between two subspecies show less evidence of structural rearrangement than do intrasubspecific hybrids (Moore & Raven, 1970). The role of structural rearrangement in the continuing differentiation of the various taxa is not known. Preliminary population studies suggest that isolated populations of *P. tagetina* may be undergoing cytological evolution and may differ from one another in the amount of translocation heterozygosity present. The amount and significance of cytological divergence among populations will be better understood when additional studies of interpopulational variation are carried out and when prime or standard types can be identified.

Although supernumerary chromosomes are now known to be common in flowering plants, having been reported in over 150 genera according to the estimate of W. V. Brown (1972), very little is known of their origin. It is likely that different types of B chro-

Table 3. **Chromosome Variability in Psilostrophe.**

Taxon	(*n*) Number	Individuals	Populations	*Translocation Heterozygosity* % Individuals	% Populations	*B Chromosomes* % Individuals	% Populations
P. bakeri	16	5	3	20	33	00	00
P. cooperi	16	10	8	40	50	00	00
P. gnaphalodes	16	13	9	46	67	00	00
P. mexicana	32	7	4	—	—	00	00
P. sparsiflora	16	5	4	00	00	00	00
P. tagetina	16	33	13	33	38	39	54
P. villosa	16	2	1	50	100	00	00

mosomes, or at least B chromosomes of different origins, occur. Misdivision and chromosomal fragmentation have been credited with giving rise to microchromosomes in *Oenothera* (Cleland, 1951) and *Caltha* (Reese, 1954). Certain supernumerary chromosomes in *Collinsia,* called "pseudosupernumerary" chromosomes by the authors, are thought to be derived from ordinary trisomics (Dhillon & Garber, 1960).

Better documented are the origins of B chromosomes in association with translocation heterozygosity in *Haplopappus* (Jackson, 1962) and *Clarkia* (Lewis, 1968; Lewis, Juhren & Mathew, 1971). In *Haplopappus* the supernumerary chromosomes apparently arise as nonessential centric fragments which persist after unequal reciprocal translocations. Whereas in *Clarkia,* B chromosomes arise from trisomics following non-disjunction in translocation heterozygotes. It is likely that in *Psilostrophe,* as in *Clarkia,* the B chromosomes arise initially from non-disjunction in translocation heterozygotes and originate, therefore, as partial trisomics. The correlation of supernumerary chromosomes with structural hybridity for translocations in *Psilostrophe tagetina* by no means proves that translocation heterozygosity was the factor contributing to the formation of B chromosomes in this taxon. It does seem, however, that carefully constructed breeding programs might add substantial evidence to reconstruct the origin of supernumerary chromosomes in this taxon.

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DEPARTMENT OF BIOLOGY
WHITMAN COLLEGE
WALLA WALLA
WASHINGTON 99362

REVISION OF CHRYSOGONUM (COMPOSITAE, HELIANTHEAE)

TOD F. STUESSY

In the course of recent studies on the subtribe Melampodiinae (Stuessy, 1973, 1975), *Chrysogonum* L. was discovered to be a small but poorly understood genus traditionally recognized (Bentham & Hooker, 1873; Hoffmann, 1890) as being related to *Moonia* Arn., *Lindheimera* A. Gray & Engl., and *Engelmannia* Torrey & Gray. One of the most perplexing problems in *Chrysogonum* has been proper generic circumscription as evidenced by the 15 included species that are morphologically and geographically diverse. In the present paper based on study of herbarium material, the taxonomic history of the genus is traced, generic relationships are discussed, many species are excluded, and the remaining single species with two varieties is described and illustrated.

TAXONOMIC HISTORY

In Linnaeus' Species Plantarum (1753) and Genera Plantarum (1754), *Chrysogonum* was first validly described to contain two herbaceous species: *C. peruvianum* and *C. virginianum.* Several years later in the Familles des Plantes of Adanson (1763), *Chrysogonum* was placed in the aggregate genus *Cargilla* Adans. along with *Melampodium* L. and portions of *Chrysanthemum* L. and *Bidens* L. Cassini (1827), following his treatment of many other genera of Compositae, described a new genus, *Diotostephus,* allied closely to *Chrysogonum* and containing the single species, *D. repens.* DeCandolle (1836) treated Cassini's *Diotostephus* as a synonym of *Chrysogonum* and recognized two species in the genus, *C. virginianum* and *C. diotostephus,* both from the southeastern United States. In addition, he referred Linnaeus' *C. peruvianum* to the genus *Zinnia* L. Bentham and Hooker (1873) counted six species of *Chrysogonum* in their Genera Plantarum, and they also included two other genera in synonymy that had been described previously: *Moonia* Arn. and *Pentalepis* F. Muell. It was at this point that the generic concept of *Chrysogonum* began to enlarge considerably, for not only were *Moonia* and

Pentalepis morphologically quite different, but they came from Ceylon and Australia, respectively. An additional isolated species, *C. philippinense,* was described from the Philippine Islands by Elmer (1906). Further enlargement and a formal emendation of the genus were made in a treatment by Brown (1935) in which he described from Rapa and the Marquesas Islands in the Pacific a new section, *Quadrimera,* that included three new shrubby species: *C. album, C. coriaceum,* and *C. rapense.* Sherff, in a treatment of some Compositae of southeastern Polynesia (1937), elevated sect. *Quadrimera* to generic status as *Oparanthus. Chrysogonum* became even more heterogeneous when Humbert (1958) added three new species from Madagascar, viz. *C. leandrii, C. madagascariense,* and *C. stenocephalum.* Recently, *Moonia* has been removed from *Chrysogonum* and referred to the subtribe Coreopsidinae (Stuessy, 1973, 1975). However, the taxa that still remain in *Chrysogonum* at the present time are morphologically very diverse and geographically widely distributed.

GENERIC RELATIONSHIPS

As treated in the present revision, *Chrysogonum* consists of only one species, *C. virginianum.* From this perspective the generic relationships of the genus are relatively clear, despite the earlier confusion caused by the presence of many morphologically diverse species.

Chrysogonum is related closely to three other genera of the subtribe Melampodiinae: *Berlandiera* DC.; *Engelmannia*; and *Lindheimera.* All of these taxa possess an unusual and unifying feature: the "achene-complex" (Rollins, 1950). This structure of the capitulum is a basally fused complex of one phyllary, one fertile female ray floret, two to three sterile hermaphroditic disc florets, and two to four receptacular paleae. At maturity of the achenes, this whole unit is dispersed together. No other genera of the Heliantheae possess this distinctive morphological feature except *Parthenium* L. and *Parthenice* A. Gray, both of which are regarded as somewhat related to *Chrysogonum,* but both have stronger affinities with the subtribe Ambrosiinae *sensu stricto* (Stuessy, 1973).

Of the three genera mentioned above as being related to *Chrysogonum, Lindheimera* is most similar in overall morphological

aspects. The chromosome number of *Lindheimera* is diploid with $n = 8$ (Turner & Johnston, 1956) whereas that of *Chrysogonum* is tetraploid with $n = 16$ (Jones, 1968; Solbrig, Kyhos, Powell & Raven, 1972). The two genera are distinguished most easily by the alternate leaves and annual habit of the former and the opposite leaves and perennial habit of the latter.

TAXONOMIC TREATMENT

Chrysogonum Linnaeus, Hort. Cliff. 424. 1737. Sp. Pl. **2:** 920. 1753. Gen. Pl. ed. 5. 391. 1754. LECTOTYPE SPECIES: *C. virginianum* L.

Cargilla Adans. Fam. Pl. **2:** 130. 1763, *pro parte.*

Diotostephus Cass. Dict. Sci. Nat. **48:** 543. 1827. TYPE SPECIES: *D. repens* Cass.

Perennial, rhizomatous herbs. Leaves opposite (sometimes appearing basal), 3(–5)-nerved toward base. Capitula terminal, solitary. Receptacle convex. Involucre cupulate, biseriate. Ray florets carpellate, fertile; ligules yellow; pappus a short abaxial collar; achenes each attached basally to a single inner phyllary, 3 paleae, and 3 sterile disc florets (termed an "achene-complex," Rollins, 1950). Disc florets hermaphroditic, sterile; corollas yellow; anthers brown to black, abaxially ridged, with basal lobes acute; style filiform; stigma undivided (sometimes slightly bifid); ovary filiform; pappus absent. Paleae oblanceolate, scarious. Chromosome number, $n = 16$.

1. **Chrysogonum virginianum** Linnaeus, Sp. Pl. **2:** 920. 1753.

Plants 3–35 cm. tall. Stems erect to decumbent, terete, green to purple, subglabrous to usually pilose with hairs up to 2 mm. long. Leaves cauline or basal, with tapering petioles 1–15 cm. long, 0.8–2 mm. diam.; blades narrowly ovate to obovate, 1.5–9.9 cm. long, 0.8–6.9 cm. wide, at apex acute to rounded, at base attenuate to subcordate, with the margin subentire to dentate, with both surfaces strigose with hairs 0.5 mm. long. Capitula 1.5–3.4 cm. diam., 0.7–1.2 cm. tall. Peduncles 2–22 cm. long, 0.7–1.8 mm. diam., pilose with hairs up to 1 mm. long. Receptacle 2–3 mm. diam. Outer phyllaries 5(–6), lanceolate to ovate, 6.5–15 mm. long, 2.5–7 mm. wide, at apex mucronate to acuminate, strigose on abaxial and upper portion of adaxial surfaces and on margin ciliate with hairs 0.5 mm. long. Inner phyllaries 5(–6), elliptic, scarious. Ray florets 5(–6); ligules elliptic, 6–17 mm.

long, 3–9 mm. wide, at the apex 3-lobed, with veins on undersurface light green; tube 0.8 mm. long, 0.4 mm. diam., puberulent; pappus a small collar 0.8 mm. tall; achenes obovoid, flattened radially, with thin longitudinal keels on both surfaces, 3–4 mm. long, 2–2.5 mm. wide, puberulent toward apex. Disc florets 25–50; throat narrowly funnelform, 2.5–2.7 mm. long, 1–1.2 mm. diam.; lobes triangular, reflexed, 0.9 mm. long, at apex subglabrous to comose; tube 0.3–1 mm. long, 0.2 mm. diam.; anthers 2 mm. long, with apical appendage tapered; style 6 mm. long, 0.2 mm. diam.; ovary 2.5 mm. long, 0.2 mm. diam.; pappus absent. Paleae 4 mm. long, 0.6 mm. wide. Chromosome number, $n = 16$.

KEY TO VARIETIES

1. Plants 15–35 cm. tall; stems erect; leaves primarily cauline (internodes well developed); primarily North Carolina, Virginia, West Virginia, and Maryland. ..... 1a. var. *virginianum*.
1. Plants 3–14 cm. tall; stems often decumbent; leaves nearly all basal (internodes very short); primarily Mississippi, Alabama, Florida, Georgia, Tennessee, South and North Carolina. ..... 1b. var. *australe*.

1a. **Chrysogonum virginianum** L. var. **virginianum** Figures 1–4.

TYPE: **Virginia.** Specific locality and date unknown, *J. Clayton "298"* ("communicata per J. F. Gronovium;" Linnaeus, 1737.) (Lectotype chosen, BM!).

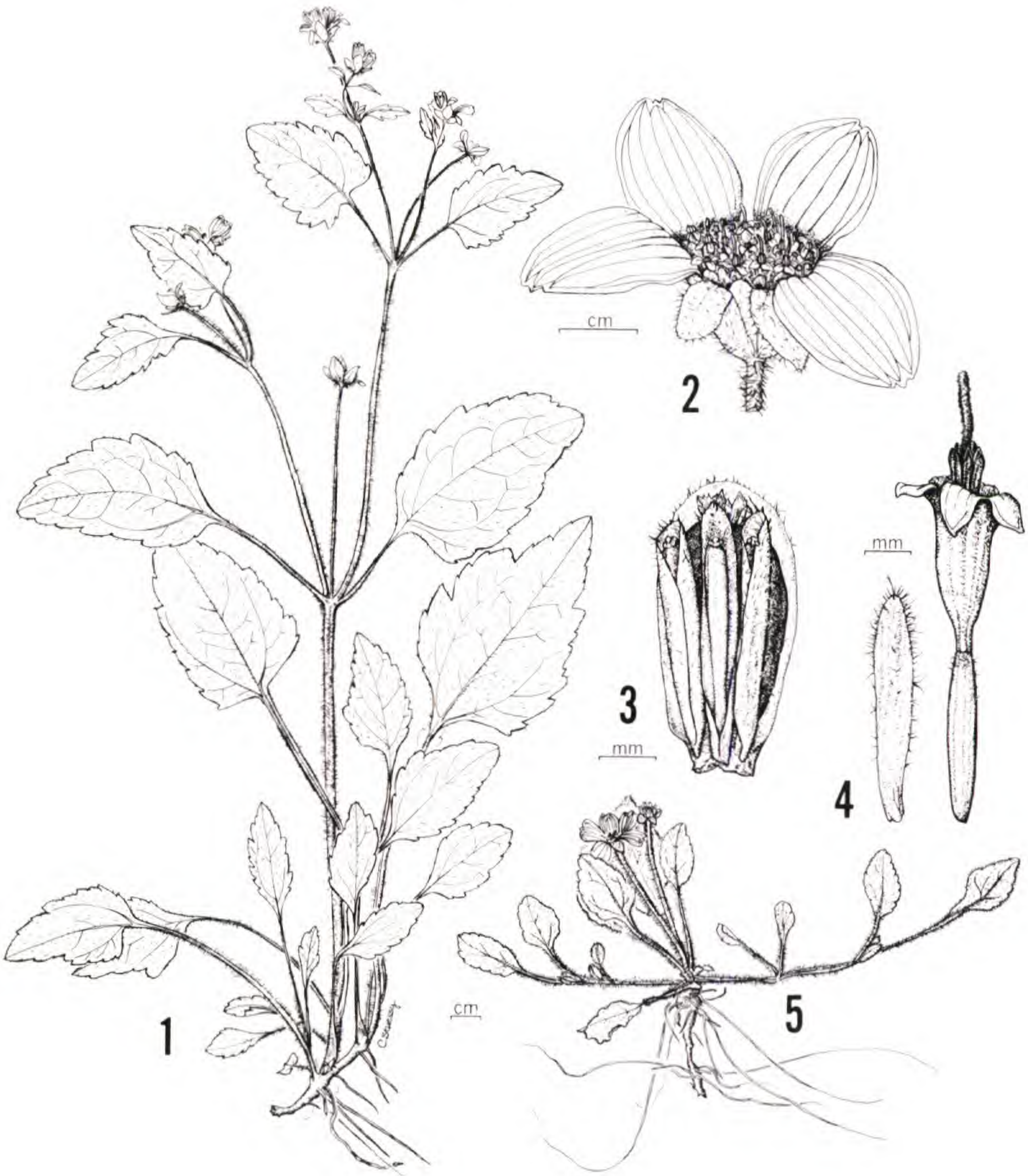
Chrysogonum virginianum L. var. *dentatum* A. Gray, Bot. Gaz. **7:** 31. 1882. TYPE: **Maryland.** Montgomery Co., High Island in the Potomac River, 6 June 1881, *J. D. Smith s.n.* (Holotype, GH!).

Plants 15–35 cm. tall. Stems erect. Leaves primarily cauline with petioles 1–15 cm. long; blades narrowly ovate to ovate, 3.5–9.9 cm. long, 2.9–6.9 cm. wide, at base attenuate to subcordate. Peduncles 2–22 cm. long. Outer phyllaries 7–15 mm. long, 3.5–7 mm. wide. Chromosome number unknown.

DISTRIBUTION — Northern piedmont and Appalachian highlands primarily in North Carolina, Virginia, West Virginia, and Maryland (Figure 6).

PRINCIPAL FLOWERING DATES — April to July.

The principal morphological feature separating *Chrysogonum virginianum* var. *virginianum* from var. *australe* is the length of the stem internodes. Longer internodes in the former taxon result in a taller plant with many cauline leaves. However, in the early



Figures 1–5. *Chrysogonum virginianum*. 1–4, var. *virginianum;* 5, var. *australe*. 1 (*Allard 8792*, US), 5 (*Palmer 35392*, GH), habit; 2, head (with one ligule removed); 3 (*Steele s.n.*, NY), achene-complex; 4, disc floret and palea. 2 & 4, *Chickering s.n.* (NY). 1 & 5 same scale.

spring when new leaves are produced, plants of var. *virginianum* are often difficult to distinguish from those of var. *australe*. An excellent example of this condition in var. *virginianum* is seen in *Fernald & Long 7980* (GH) collected on 5 April in southeastern Virginia in which the long stems (over 30 cm.) from last year are still attached to the cluster of new basal leaves and young flowering heads all under 10 cm. in height. Despite this difficulty, the two recognized varieties can usually be distinguished with confidence. A number of morphological intermediates exist, however, and these have been separately cited below and plotted in Figure 6.

Chrysogonum virginianum var. *dentatum* (Gray, 1882), with its more strongly serrate leaf margins, is regarded here as nothing more than a minor morphological variant undeserving of formal taxonomic recognition.

REPRESENTATIVE SPECIMENS (var. *virginianum*). — **District of Columbia.** 10 Oct 1876, *Chickering s.n.* (NY). **Maryland.** MONTGOMERY CO.: Great Falls, 4 Apr 1968, *Harding s.n.* (NCU). **North Carolina.** ANSON CO.: 7 mi N of Lilesville, *Radford 43659* (NCU). CASWELL CO.: 1 mi N of Concord Church, SSW of Locust Hill, *Bell 11875* (NCU). FORSYTH CO.: Winston-Salem, *Wyatt 804* (NCU). ORANGE CO.: Battle Park, Chapel Hill, May 1939, *Ward & Christenberry s.n.* (NCU). ROAN CO.: near Spencer, *Palmer 39977* (GH). WAKE CO.: 4 mi E of Apex, *Ahles & Carswell 58717* (NCU). **South Carolina.** FLORENCE CO.: 0.5 mi SW of Pee Dee River, *Bell 6138* (NCU). **Virginia.** AMHERST CO.: along John's Creek near James River, *Freer 1433* (GH). BUCKINGHAM CO.: 2.6 mi NE of county line on Co. Rd. 605, *Ramsey, Hooks, Ruska & Waggoner 7649* (NCU). HALIFAX CO.: 12 mi E of Danville, *Fosberg 15382* (GH). MONTGOMERY CO.: 2 mi SE of Ellett, *Kral 10227* (NCU). PRINCE GEORGE CO.: Garysville, *Fernald & Long 7980* (GH). SHENANDOAH CO.: S end of Short Mt., *Allard 8792* (US). YORK CO.: N shore of Tutters Neck Pond, SE of Williamsburg, *Grimes 3817* (NY). **West Virginia.** GREENBRIER CO.: White Sulphur Springs, 1838, *Buckley 5* (GH, US). MONROE CO.: near Organ Cave, 1 Jul 1941, *Sharp s.n.* (WVA). TYLER CO.: near Middlebourne, 8 May 1937, *Brooks & Margolin s.n.* (WVA).

REPRESENTATIVE SPECIMENS (morphological intermediates). — **District of Columbia.** *Sylvester 22* (NY). **Georgia.** DE KALB CO.: Stone Mt., 1–18 May 1895, *Small s.n.* (NY). **Maryland.** PRINCE GEORGES CO.: Glen Echo Heights, 3 May 1914, *Steele s.n.* (GH). **North Carolina.** BRUNSWICK CO.: 0.3 mi S of US 74 on NC 40, *Bell & Kim 263* (NCU). DURHAM CO.: Duke Univ. Campus, *Barrell 5* (NY). GUILFORD CO.: 2 mi N of Gibsonville, *Bell 11703* (NCU). NEW HANOVER CO.: Wrightsville, *Ahles & McCrary 58896* (NCU). **Pennsylvania.** FULTON CO.: Tonotoway Creek, 19 May 1956, *Krouse s.n.* (NCU). **South Carolina.** CHARLESTON CO.: Porchers Bluff, Christ Church Parish, *Mearns 58* (US). RICHLAND CO.: near Columbia, 27 Apr 1937, *Chapman s.n.* (GA). **Virginia.** AUGUSTA CO.: 1 mi N of Craigsville, *Steele 107* (US). ROCKBRIDGE CO.: Natural Bridge, 28 Apr 1886, *Kennedy s.n.* (GH). **West Virginia.** RICHIE CO.: near Cairo, Apr 1930, *Goodwin s.n.* (WVA).

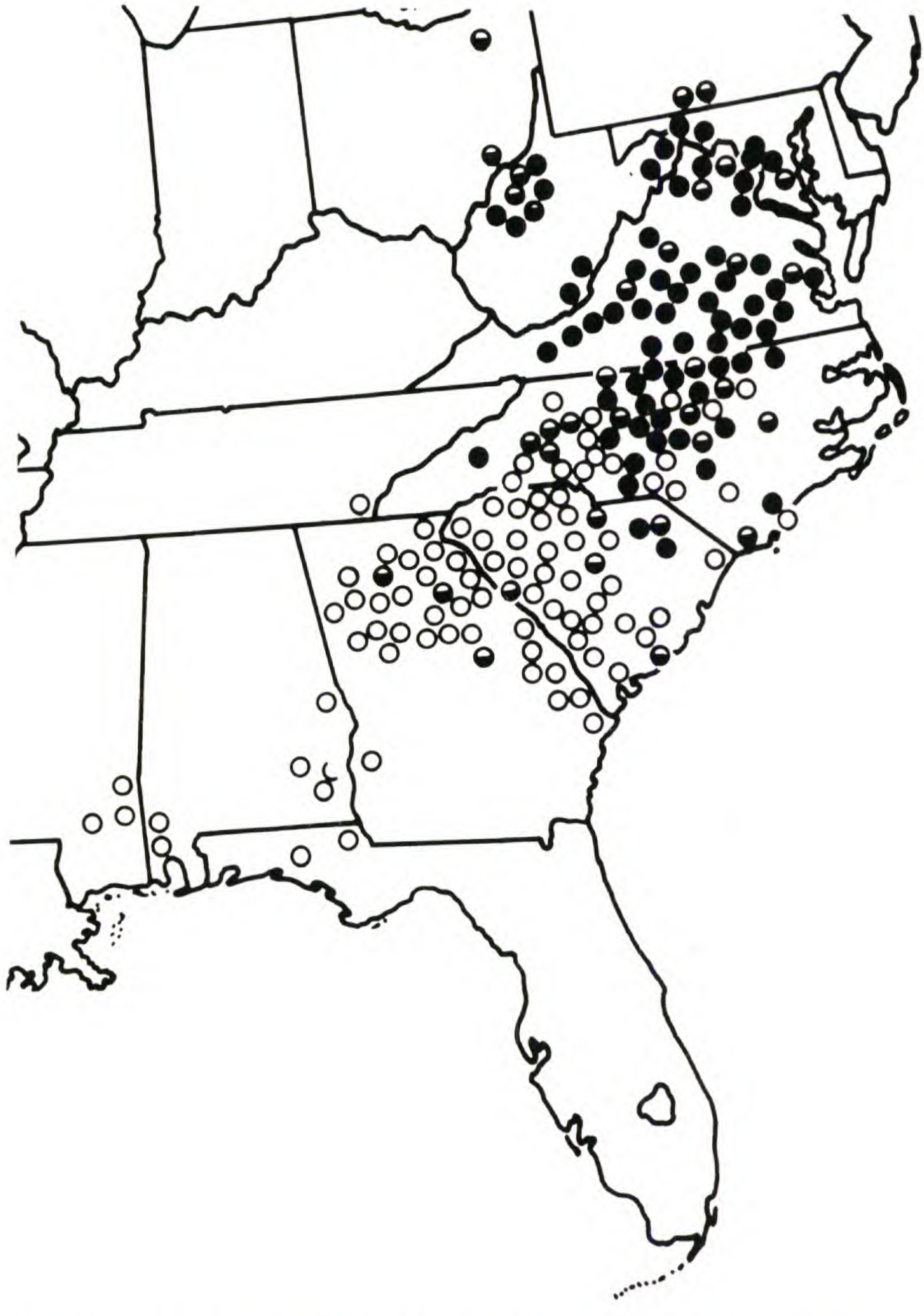


Figure 6. Map of southeastern United States showing distribution of *Chrysogonum virginianum* var. *virginianum* (black dots), var. *australe* (circles), and morphological intermediates (half-closed circles).

1b. **Chrysogonum virginianum** L. var. **australe** (Alexander ex Small) Ahles, Jour. Elisha Mitchell Sci. Soc. **80:** 173. 1964. Figure 5.

Chrysogonum australe Alexander ex Small, Man. Southeast. Fl. 1415. 1933. TYPE: **Florida.** Jackson Co., "Dry woods, somewhat calcareous, about a mile east of Marianna" 16 March 1925, *R. M. Harper s.n.* (Holotype, NY!; isotypes, GH!, US!).

Diotostephus repens Cass. Dict. Sci. Nat. **48:** 544. 1827. TYPE: "Nous avons fait cette description, générique et spécifique, sur un très-petit èchantillon sec, incomplet, en mauvais ètat, et dont nous ignorons l'origine," (Holotype, P? not located).[1]

Chrysogonum diotostephus DC. Prodr. **5:** 510. 1836. *Nom. illegit.*, based on type of *Diotostephus repens* Cass.

Plants 3–14 cm. tall. Stems often decumbent. Leaves primarily basal with petioles 2–7 cm. long; blades ovate to obovate (sometimes narrowly ovate), 1.5–7 cm. long, 0.8–4 cm. wide, at base attenuate. Peduncles 2–9 cm. long. Outer phyllaries 6.5–9 mm. long, 2.5–4 mm. wide. Chromosome number, $n = 16$.

DISTRIBUTION. — Coastal plain and southern piedmont primarily in Mississippi, Alabama, Florida, Georgia, Tennessee, South and North Carolina (Figure 6).

PRINCIPAL FLOWERING DATES. — March to May.

This taxon was first described as a species by Cassini (1827) and then by Small (1933) from a collection from Jackson Co., Florida. Later, Ahles (1964) proposed the rank of variety which is the perspective adopted in the present treatment. The distribution of *Chrysogonum virginianum* var. *australe* is quite distinct from that of var. *virginianum* (Figure 6), but intermixing occurs commonly, particularly in North Carolina. *Chrysogonum virginianum* var. *australe* is located primarily on the coastal plain and southern piedmont, whereas var. *virginiańum* is more concentrated on the northern piedmont and Appalachian highlands.

REPRESENTATIVE SPECIMENS. — **Alabama.** LEE CO.: Auburn, 10 Apr 1896, *Earle & Underwood s.n.* (NY). **Florida.** JACKSON CO.: along Chipola River at Marianna, *Godfrey 5443D* (NY). **Georgia.** BARTOW CO.: 2¼ mi NW of Acworth, *Duncan 8033*

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[1]Even though type material has not been located, the detailed description of *Diotostephus repens* by Cassini (1827), in which he mentions among other features the decumbent stems and clusters of condensed leaves, suggests strongly that the specimen before him was of *Chrysogonum virginianum* var. *australe*.

(GA). CLARKE CO.: near Lake Kirota at edge of Univ. Georgia campus, Athens, *Cronquist 4386* (GA, GH, US, NY). DE KALB CO.: open woods at base of Stone Mt., *Curtiss 6766* (GA, GH, NY, US). FORSYTH CO.: banks of the Chattahoochee River, *Duncan 5252* (GA). HARALSON CO.: Tallapoosa, *Way 50* (US). JASPER CO.: 3.5 mi SW of Monticello, *Duncan 22297* (GA). OGLETHORPE CO.: 7 mi NE of Lexington, *Cronquist 4973* (GA). RANDOLPH CO.: Little Pumpkin Creek just W of Lumpkin Rd., *Thorne & Muenscher 7784* (GA, GH, NY, US). WILKES CO.: 6 mi NE of Tignall, *Cronquist 4987* (GA, GH, NY). **Mississippi.** FORREST CO.: Ragland Hills, 12–13 mi SE of Hattiesburg, *Rogers 2056-B* (NCU). **North Carolina.** ALAMANCE CO.: Haw River, *Carlton 56* (NCU). CHATHAM CO.: near Emmaus Baptist Church, 3 mi from jct. of Co. Rte. 1346 & hwy 87, *Massey, Boufford & Williams 3833* (NCU). GASTON CO.: 2 mi W of Lucia, *Bell 1940* (NCU). MOORE CO.: near Carthage, 14 May 1928, *Harriot s.n.* (NCU). POLK CO.: Tryon, *Peattie 1618* (NCU). ROWAN CO.: Yadkin River near US 29 bridge, *Horton 694* (GA). VANCE CO.: W of Henderson, *Bell & Ahles 10888* (NCU). **South Carolina.** ABBEVILLE CO.: ¼ mi from Due West, *Anderson A-29* (NCU). BAMBERG CO.: W of Denmark, *Ahles & Haesloop 22176* (NCU). CALHOUN CO.: 4 mi SE of Lone Star, *Radford 9340* (NCU). DORCHESTER CO.: Four Holes Swamp on US 178, *Ahles & Haesloop 21913* (NCU). GREENWOOD CO.: Tolbert Branch, *Radford 20136* (NCU). LANCASTER CO.: 10 mi NNW of Lancaster, *Hardin & Duncan 15589* (GA). NEWBERRY CO.: Mills Creek (on SC 59), *Bell 7017* (NCU). RICHLAND CO.: Crane Creek near Cola, 29 Mar 1937, *Chapman s.n.* (GA). YORK CO.: S of Hickory Grove, *Ahles & Haesloop 22894* (NCU). **Tennessee.** BRADLEY CO.: on the Ocoee River, *Kearney 98* (US).

EXCLUDED NAMES

Chrysogonum album F. Br. Bull. B. P. Bishop Mus. **130:** 342. 1935. TYPE: **French Polynesia:** Marquesas Islands, Hiva Oa, Feani, 850 m, 15 Dec. 1921, *F. & E. Brown 1088* (Holotype, BISH!). = **Oparanthus albus** (F. Br.) Sherff, Occas. Papers B. P. Bishop Mus. **12**(19): 12. 1937.

Chrysogonum arnottianum (Wight) C. B. Clarke, Compos. Ind. 132. 1876. *Moonia arnottiana* Wight, Ic. **3**(4): 9. *t. 1105.* 1846. TYPE: **India:** MADRAS: "Neilgherries and Pulney mountains in clumps of jungle — on the former common near the Avalanche Bungalow and in almost every clump of jungle from thence to near Sisparah," Sep. 1836 & Aug. 1845, *R. Wight 1610* [herbarium number] (Lectotype,K!; isotypes, GH! K! NY!; fragments from K isotype, US!). = **Moonia heterophylla** Arn. Nov. Actorum Caes. Leop.-Carol. German Nat. Cur. **18:** 349. 1836.

Chrysogonum L. sect. **Baltimora** (L.) Baillon, Hist. Fam. Plant. 232. 1882. = **Baltimora** L. Mant. 158. 1771.

Chrysogonum coriaceum F. Br. Bull. B. P. Bishop Mus. **130:** 344. 1935. TYPE: **French Polynesia:** Tubuai Islands, Rapa, 1922, *E. H. Quayle X* (Holotype, BISH!). = **Oparanthus coriaceus** (F. Br.) Sherff, Occas. Papers B. P. Bishop Mus. **12**(19): 11. 1937.

Chrysogonum dichotomum Vahl. ex West, Bidr. Ste Croix. 230. 1794. *nom. nud.*

Chrysogonum ecliptoides (F. Muell.) F. Muell. Census Austral. Pl. 83. 1882. *Pentalepis ecliptoides* F. Muell. Trans. Bot. Soc. Edinburgh **7:** 496. 1863. TYPE: **Australia:** "Arnhem's Land, in planitiebus originem fluvii Victoriae versus," 28 Mar. 1856, *P. Wolcott & M. Brown s.n.* (Holotype, not located). Although the holotype has not been located, a collection from Australia has been seen that was examined and cited by Bentham (1867): *F. Mueller s.n.*, Hooker's and Sturt's Creeks; K! US! [fragment]. = aff. **Blainvillea.**

Chrysogonum heterophyllum (Arn.) C. B. Clarke, Compos. Ind. 132. 1876. = **Moonia heterophylla** Arn. Nov. Actorum Caes. Leop.-Carol. German Nat. Cur. **18:** 349. 1836. TYPE: **Ceylon:** specific locality unknown, 1834–36, *Mrs. Walker s.n.* (Holotype, K; isotype, GH!).

Chrysogonum leandrii H. Humb. Not. Syst. Paris **15:** 256. 1958. TYPE: **Madagascar:** "environs de Tsiandro (Bemaraha)," 9 Feb. 1933, *J. Leandri 808* (Holotype, P!). = **Wedelia** sp.

Chrysogonum madagascariense H. Humb. Not. Syst. Paris **15:** 256. 1958. TYPE: **Madagascar:** "Bois tropophiles de l'Ouest sur calcaire (éocène) prés de Majunga," Mar. 1925, *Perrier de la Bâthie 17278* (Holotype, P!). = **Wedelia** sp. This taxon is very similar to *Baltimora geminata* (Brandg.) Stuessy in both vegetative and floral features. The former differs, however, in the very small heads with fewer and rhombic phyllaries, in the longer anthers (1.4 mm.), in the very short paleae (1 mm.), and in the absence of pappus on ray and disc florets. The close resemblance of this taxon to both *Baltimora* and *Wedelia* Jacq. re-emphasizes the need for a careful study of *Wedelia* in relation to other genera such as *Aspilia* Thou., *Baltimora, Rensonia* S. F. Blake, and *Schizoptera* Turcz.

Chrysogonum L. sect. **Moonia** (Arn.) Baillon, Hist. Fam. Plant. 232. 1882. = **Moonia** Arn. Nov. Actorum Caes. Leop.-Carol. German Nat. Cur. **18:** 348. 1836.

Chrysogonum perrieri (H. Humb.) H. Humb. Fl. Madag. Fam. 189. **3:** 633. 1963. *Wedelia perrieri* H. Humb. Mem. Soc. Linn. Paris **25:** 301. 1923. TYPE: **Madagascar:** Andranomavo (Ambongo), Feb. 1903, *Perrier de la Bâthie 1517* (Holotype, P!). = **Wedelia** sp.

Chrysogonum peruvianum L. Sp. Pl. 920. 1753. TYPE: **Peru:** date unknown, *Jussieu s.n.* (Holotype, P-JU). = **Zinnia peruviana** (L.) L. Syst. ed. 10. 1221. 1759. *fide* Torres (1963).

Chrysogonum philippinense Elmer, Leaflets Philipp. Bot. **1:** 161. 1906. TYPE: **Philippine Islands:** Culion Island, "a dry open grassy valley at Halsey Harbor," Dec. 1902, *E. D. Merrill 514* (Holotype, probably PNH; isotype, NY!). = **Anisopappus chinensis** (L.) Hook. & Arn. Bot. Beech. Voy. 196. 1837.

Chrysogonum procumbens (DC.) F. Muell. Census Austral. Pl. 83. 1882. *Wollastonia procumbens* DC. Prodr. **5:** 548. 1836. TYPE: **Australia:** "upon the cliffy shores of the islands of the north coast of Australia," 15 Apr. 1818, *A. Cunningham 57* (= *244*) (Holotype, G-DC; IDC 800. **937:** III. 7!; isotypes, K[2]!). = **Wedelia** sp.

Chrysogonum L. sect. **Quadrimera** F. Br. Bull. B. P. Bishop Mus. **130:** 341. 1935. = **Oparanthus** Sherff, Occas. Papers B. P. Bishop Mus. **12**(19): 9. 1937.

Chrysogonum rapense F. Br. Bull. B. P. Bishop Mus. **130:** 343. 1935. TYPE: **French Polynesia:** Tubuai Islands, Rapa, Maitua, "on talus with other trees and ferns," 180 m., 10 Oct. 1921, *A. M. Stokes 337* (Holotype, BISH!). = **Oparanthus rapensis** (F. Br.) Sherff, Occas. Papers B. P. Bishop Mus. **12**(19): 11. 1937.

Chrysogonum stenocephalum H. Humb. Not. Syst. Paris **15:** 257. 1958. TYPE: **Madagascar:** "massif de l'Ivakoany au nord de Tsivory, sur granite," 1300 m., Dec. 1933, *H. Humbert 12234* (Holotype, P!; paratype [*H. Humbert 14216*], P!). = **Wedelia** sp.

Chrysogonum trichodesmoides (F. Muell.) F. Muell. Census Austral. Pl. 83. 1882. *Pentalepis trichodesmoides* F. Muell. Trans. Bot. Soc. Edinburgh **7:** 496. 1863. TYPE: **Australia:** "In vallibus rupestribus sinus Nikol Bay," 1861, *P. Walcott s.n.* (Holotype, K!). = aff. **Blainvillea.**

Chrysogonum L. sect. **?Trigonospermum** (Less.) Baillon, Hist. Fam. Plant. 233. 1882. = **Trigonospermum** Less. Syn. Gen. Comp. 214. 1832.

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DEPARTMENT OF BOTANY
OHIO STATE UNIVERSITY
COLUMBUS, OHIO 43210

MORPHOLOGICAL INTERGRADATION OF VARIETIES OF BIDENS ARISTOSA (COMPOSITAE) IN NORTHERN ARKANSAS

BARNEY L. LIPSCOMB AND EDWIN B. SMITH

Bidens polylepis Blake (Compositae) is a widespread, fall-blooming, herbaceous perennial of low ditches and waste ground in the eastern United States. It was described by Nuttall (as *Coreopsis involucrata*) in 1834. It is very similar to *B. aristosa* (Michx.) Britton, another widespread species of similar range, differing (purportedly) from *B. aristosa* in its more numerous, larger, and coarsely pubescent outer phyllaries (those of *B. aristosa* few, small, and nearly glabrous) and its narrower achenes. The two species include parallel varieties.

While several authors have expressed doubts as to the relative distinctness of *Bidens polylepis* and *B. aristosa* (e.g., Cronquist, 1952; Steyermark, 1963; Smith, 1973), *B. polyepis* has been treated at the species level by taxonomists (including the latest authority on the genus; Sherff, 1937) until very recently. Wunderlin (1972) formally proposed that *B. polylepis* be reduced to a variety of the older *B. aristosa,* as *B. aristosa* (Michx.) Britt. var. *retrorsa* (Sherff) Wunderlin, a reduction that seemed perfectly reasonable to the present authors. Wunderlin, however, made the new combinations without presenting supporting data. Intergradation between *B. aristosa* var. *aristosa* and var. *retrorsa* had been noted informally by the authors in Arkansas and Texas material. A study of this intergradation in populations of *B. aristosa* in northern Arkansas was undertaken with the intention of providing formal supporting data for Wunderlin's combinations.

MATERIALS AND METHODS

Two populations of *Bidens aristosa* in northern Arkansas were selected for study. Each population included several hundred individuals. Population I was located in Fayetteville, Washington County, in northwestern Arkansas, one and one-half miles west of jct. US 71 bypass & highway 16 west. Population II was located in Baxter County in north central Arkansas about 125 miles ENE of population I, one mile west of Mt. Home on highway 5.

Twenty-five plants in each population were sampled. Entire small plants or the top 30–40 cm. of large plants were pressed, and the height of each plant was recorded. Where less than the whole plant was collected, the individuals were tagged so that mature achenes could be harvested at a later visit. Plants were selected by walking through the population and collecting those of various heights at intervals of three steps (approximately 2 meters). A wide range in height was emphasized because it was noticed that relatively short and relatively tall plants appeared to differ significantly in phyllary number from the medium-sized plants in a single population.

The four key characters commonly used to separate the varieties (cf. Steyermark, 1963) were measured from the dried specimens: (1) number of outer phyllaries, (2) condition of their margins (degree of pubescence), (3) length of the outer and inner phyllaries, and (4) width of the inner and outer achenes. The varieties of *Bidens aristosa* (treated as species by Steyermark) are compared in the four key characters in Table I (extracted from Steyermark, 1963).

Table I. **Differences between varieties of Bidens aristosa.**

Character	var. *aristosa*	var. *retrorsa*
No. outer phyllaries	8–12	12–25
Margins outer phyllaries	smooth or moderately finely hairy	coarsely hairy
Length outer phyllaries	4–7 mm., mainly shorter than the inner phyllaries	7–20 mm., mostly longer than the inner phyllaries
Mature achene width	outer: 3.3–5.2 mm. inner: 2.5–4.6 mm.	outer: 2.5–3.8 mm. inner: 1.8–2.8 mm.

From earlier inspection it was known that phyllary number varied on different heads of the same plant. To see if the position of the head on the plant influenced phyllary number, the number of outer phyllaries was counted on several heads per individual. Counts of phyllary number were made on the terminal head of the main stem (T), the primary lateral head of the branch from the first node below the main terminal (L1), second node below the main terminal (L2) etc. through the fourth node (L4). Additionally, the phyllary number of the secondary lateral heads below each of the primary lateral heads (1a, 2a, 3a etc.) were counted; see Figure 1 for a diagram of these positions.

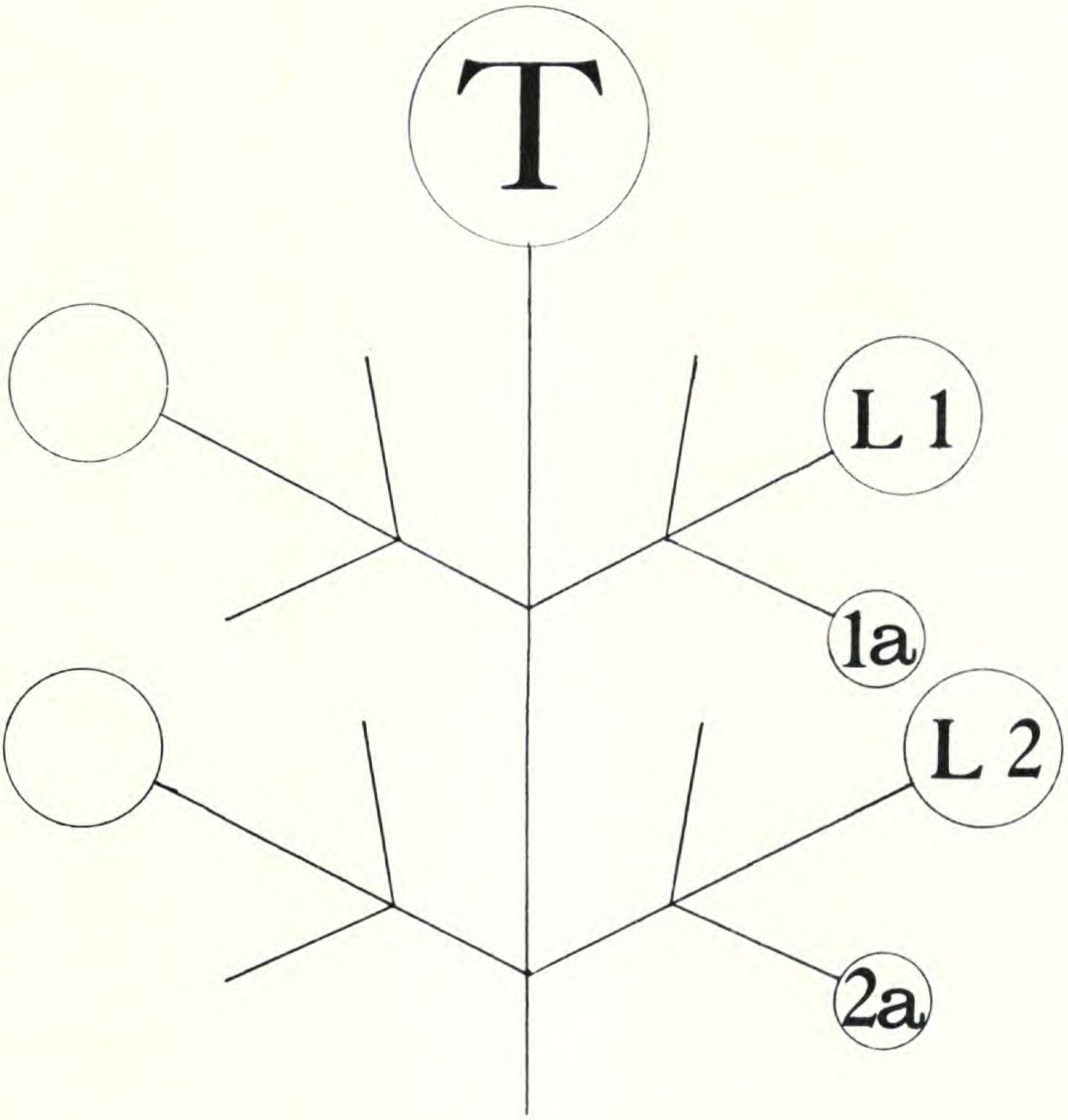

Figure 1. Schematic drawing of positions of heads measured in *Bidens aristosa* samples. T = main terminal; L1 = primary lateral head of node 1, L2 = primary lateral head of node 2, etc.; 1a = secondary lateral of node 1, 2a = secondary lateral of node 2, etc.

A scale of 1–5 was devised to rank the relative pubescence of the outer phyllaries of the plants (Figure 2). The lengths of the outer and inner phyllaries were converted to a ratio by dividing the outer length by the inner length. *Bidens aristosa* var. *aristosa* (outer phyllaries mainly shorter than inner) should exhibit a number of less than 1.0 under this scheme, while var. *retrorsa* (outer phyllaries mostly longer than inner) would exhibit numbers of greater than 1.0.

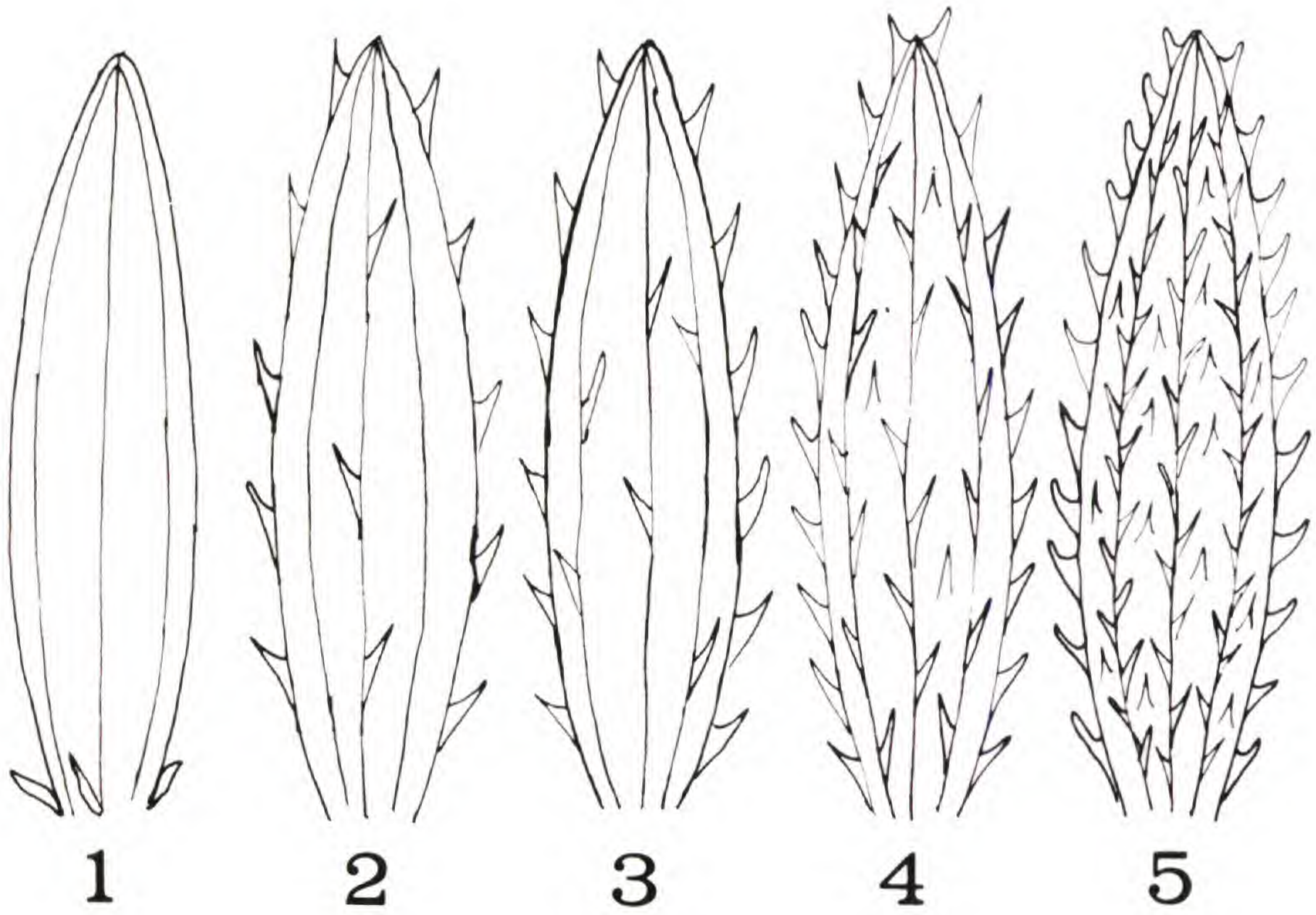

Figure 2. Scale of relative pubescence of the outer phyllaries in *Bidens aristosa* samples, from essentially glabrous (1) to densely hairy (5).

Specimens collected in the field for this study are on file at UARK. Herbarium specimens of *Bidens aristosa* (including those labeled *B. polylepis*) at UARK and SMU were examined for variation in the key characters.

RESULTS AND DISCUSSION

Tables II and III show the measurements of the four characters for populations I and II, which are listed according to height of the plants. When the height of the plant is compared with the number of outer phyllaries per head (Tables II & III), there is generally little correlation; but some positive correlation is exhibited on the extremes of the height range: plants less than 38 cm. tall (Table II) or more than 115 cm. tall (Table III) tend to have a decreased (very short) or increased (very tall) number of outer phyllaries. If one tends to pick up smaller plants that fit a press more evenly, one would generally be selecting plants with a smaller number of outer phyllaries; if one "top-snatched" larger plants, one would be unwittingly selecting plants with generally a larger number of outer phyllaries.

Table II. **Height, outer phyllary pubescence & number per head, outer to inner phyllary ratio, and achene width of Bidens aristosa sampled from population I.** (* = Unable to relocate in the field.)

Plant No.	Height, cm.	Range, No. of outer phyllaries	Range, ratio O:I phyllaries	Range of outer phyllary pubescence	Average width of inner achenes mm.	Average width of outer achenes mm.
1	105	11–13	0.8–1.2	4–5	3.0	3.7
2	98	11–15	1.0	3	2.5	3.7
3	88	9–13	0.9–1.0	3	2.2	3.0
4	85	9–13	1.0–1.4	3	1.9	3.4
5	85	12–18	0.8–1.5	3–5	2.6	3.9
6	73	11–14	1.3–1.4	3–5	*	*
7	58	12–14	1.1–1.3	3–4	2.5	3.8
8	55	13–15	0.8–1.3	3–4	2.5	3.5
9	55	9–10	1.0–1.6	5	2.5	3.6
10	50	10–12	1.4–1.6	2–3	3.0	3.8
11	50	12–15	0.9–1.2	3–5	2.3	3.0
12	48	10–13	1.1	2–4	2.4	3.2
13	45	12–14	1.0–1.6	3–4	*	*
14	43	9–11	1.1–1.2	3–4	2.9	3.4
15	43	9–10	1.1–1.5	3	2.4	3.4
16	43	11–12	1.1–1.6	3	2.8	3.4
17	43	10–13	0.9–1.4	3	2.9	3.6
18	40	10–12	1.0–1.1	2–3	2.1	2.9
19	38	13	1.3–1.5	3	2.8	3.6
20	38	9–10	1.4–1.7	3	2.5	3.6
21	34	8	1.1–1.2	4	2.5	2.8
22	34	10–12	1.1–1.5	3	2.8	3.8
23	34	10–12	1.3–1.5	2–3	*	*
24	32	7–10	1.6–1.7	2–3	*	*
25	20	7–13	0.9–1.6	2–3	3.4	3.8

Table III. **Height, outer phyllary pubescence & number per head, outer to inner phyllary ratio, and achene width of Bidens aristosa sampled from population II.** (* = Unable to relocate in the field.)

Plant No.	Height, cm.	Range, No. of outer phyllaries	Range, ratio O:I phyllaries	Range of outer phyllary pubescence	Average width of inner achenes mm.	Average width of outer achenes mm.
1	138	13–18	1.0–1.2	3–4	*	*
2	133	13–17	0.8–1.2	5	2.6	4.0
3	130	14–22	0.9–1.2	4–5	2.0	3.6
4	129	14–23	0.7–1.0	3–4	2.7	3.6
5	115	11–15	0.9–1.2	3–5	2.1	3.2
6	105	10–15	0.7–1.0	4–5	2.4	3.2
7	100	13–16	0.8–1.2	3–4	2.4	3.2
8	100	11–14	0.9–1.2	3–5	2.4	3.7
9	100	10–17	0.9–1.3	3–4	2.5	3.6
10	95	11–14	0.8–1.1	5	2.6	3.3
11	95	9–14	0.7–1.0	3–4	2.8	3.6
12	95	10–16	0.8–1.1	4–5	2.5	3.1
13	90	10–14	0.9–1.2	3–5	2.6	3.8
14	88	12–16	0.9–1.6	5	2.7	4.1
15	83	13–16	1.0–1.2	4–5	*	*
16	75	13–14	0.8–1.1	3–5	*	*
17	75	11–14	0.8–1.1	3–4	3.1	4.1
18	73	12–17	0.6–1.1	4–5	2.0	4.2
19	70	13–18	1.0–1.2	4–5	2.6	4.2
20	68	14–18	0.8–1.4	4–5	2.4	3.5
21	60	10–14	0.9–1.1	3–4	3.0	3.5
22	60	11–13	0.6–0.9	4	3.0	3.9
23	55	12–15	0.9–1.0	3–4	1.8	3.5
24	53	9–15	0.8–1.1	3–4	2.7	3.7
25	46	13	1.0–1.1	3	2.2	3.8

On the basis of the range in number of phyllaries on a single plant (Tables II & III), particular individuals in the Arkansas populations could be counted as either variety. Based on the outer phyllary number, some plants are all one variety, some plants all the other variety, and many could be counted as either variety. It is clear that there is considerable overlap in Arkansas material for this character and that it is therefore of little taxonomic value in separating the varieties in Arkansas.

The phyllary pubescence character is also of little taxonomic value in separating the varieties in Arkansas. While all phyllaries on a head are the same, those on other heads of the same plant can be more or less hairy (Tables II & III).

The ratio of outer phyllary length to inner phyllary length is variable on individual plants (Tables II & III). Some heads measured on the same plant had the outer phyllaries longer and others had the inner phyllaries longer. This character is so variable on a single plant that it cannot be used as a distinguishing characteristic for the varieties.

Achene width is not used in the various manuals as often as the other characters. It is probably just as well because the measurements overlap between the two varieties. Achene widths measured on the Arkansas populations mostly straddled the area of overlap.

Tables IV and V provide data that indicate that the number of outer phyllaries per head is correlated with position of the head on the plant. Frequently (particularly in population II; Table V), the head terminating the main stem has more phyllaries than any other head on the plant. This head is the first one to bloom. Later heads terminating lateral branches (primary laterals; L1, L2, etc.) were found to be about the same for outer phyllary number regardless of node position, but had fewer outer phyllaries as a group than the terminal head. Secondary laterals (1a, 2a, etc.) had a smaller number than primary laterals. Thus, a single plant (on the basis of outer phyllary number) could key to *Bidens aristosa* var. *retrorsa* or var. *aristosa* depending on whether one counted the terminal, primary lateral, or secondary lateral heads.

Data presented in Tables II–V indicate that all of the four characters commonly used to separate the two varieties are unstable or highly variable, and that there is copious intergradation

Table IV. **Number of outer phyllaries per head at different positions on the plant, for the Bidens aristosa sample of population I.** (Blank spaces represent undeveloped heads or heads damaged in pressing some individuals. The positions (T, T1, etc.) are explained in the text and illustrated in Figure 1.)

	T	L1	L2	L3	L4	1a	2a	3a	4a	Total	N	Av.
1	12	15	13	12	11	14	13	12	13	115	9	12.7
2	11	12		12		9		13		57	5	11.4
3		12	12			15	14			53	4	13.2
4	8	8								16	2	8.0
5	10		12	11			10	10		53	5	10.6
6	7			12	10	7		13	9	58	6	9.6
7		15		15		14		13		57	4	14.2
8	12	12			13	11			11	59	5	11.8
9		13		13		12		14		52	4	13.0
10	18	15		15		12		13		73	5	14.6
11	9	11						13		33	3	10.0
12	10		10				12			32	3	10.6
13	10	13				12				35	3	11.6
14		10				9	11			30	3	10.0
15	9						10	10		29	3	9.6
16		9	9			10				28	3	9.3
17	12	11								23	2	11.5
18	12	10	13		11		11		10	67	6	11.1
19		10	8		7	9	8		7	49	6	8.1
20	11	10				10		10		41	4	10.2
21	10	11					9			30	3	10.0
22	13	13	13			13				52	4	13.0
23	10			10	10		12		9	51	5	10.2
24	11	11	14		11				11	59	5	11.8
25	14			12	12	12		12	11	72	6	12.0
Total	209	220	104	104	85	169	110	133	81			
N	19	19	9	9	8	15	10	11	8			
Av.	11.0	11.5	11.5	12.4	10.6	11.2	11.0	12.0	10.1			

Table V. **Number of outer phyllaries per head at different positions on the plant, for the Bidens aristosa sample of population II.** (Blank spaces represent undeveloped heads or heads damaged in pressing some individuals. The positions (T, T1, etc.) are explained in the text and illustrated in Figure 1).

	T	L1	L2	L3	L4	1a	2a	3a	4a	Total	N	Av.
1	18	16	14				13			61	4	15.2
2	14	11	16	13	13		13		10	90	7	12.8
3	14	13	12	16	16		14	13	13	111	8	13.8
4	22	17	16	16	15		15	14		115	7	16.4
5	13	15	13	13	13		13	13	11	104	8	13.0
6	18	15	15	16	16		14	14		108	7	15.4
7	13	12	11	13	12		11			72	6	12.0
8	12	15	13							40	3	13.3
9	11	10	10			9				40	4	10.0
10	15	14	14	14	14	13	14	14	13	125	9	13.8
11	16	15	15			13	13			72	5	14.4
12	17	14	14	15	16	15	12	14	13	130	9	14.4
13	13	13	12	14	12	12	12	11	10	109	9	12.1
14	14	13	14	14		12	10			77	6	12.8
15	13	14	13	13	13	12	12	11	12	113	9	12.5
16	14	15	13	10	15	11	15	11	11	115	9	12.7
17		14				11				25	2	12.5
18	17	14	16	15	15	13	13	13		116	8	14.5
19		13				13				26	2	13.0
20	14	13	14	13		15	16			85	6	14.1
21		12	13	14		9	10	10		68	6	11.3
22	23	19	18	18		15	15	14		122	7	17.4
23	14	17		15		13	13	10		82	6	13.6
24	14	13	13	14	13	13	13	14	14	121	9	13.4
25	14	14	13	12	12	13	13	11	11	113	9	12.5
Total	333	351	302	268	195	212	274	187	118			
N	22	25	22	19	14	17	21	15	15			
Av.	15.1	14.0	13.7	14.1	13.9	12.4	13.0	12.4	11.8			

of *Bidens aristosa* var. *aristosa* and var. *retrorsa* in northern Arkansas. Frequently in Arkansas material, certain plants are similar to var. *aristosa* in one or two characters and to var. *retrorsa* in the remaining characters. Inspection of herbarium material from Arkansas and Texas indicates that the intergradation is not limited to northern Arkansas, but is widespread. Although the field sampling in this study was limited to northern Arkansas, we believe that the results are applicable to the entire eastern United States range of the two varieties. The two varieties are separated in manuals for other areas (e.g., Radford et al., 1968; Fernald, 1950; Correll & Johnston, 1970) on some or all of the same characters as those found to be inconstant in this study. While this study was undertaken to provide formal supporting data for Wunderlin's reduction of *B. polylepis* to *B. aristosa* var. *retrorsa,* the copious intergradation of varieties *aristosa* and *retrorsa* in northern Arkansas (and probably elsewhere) and the inconstancy of the key characters even for different parts of the same plant have convinced us that we are dealing with a single taxonomic unit which at the varietal level is polymorphic in these four characteristics.

We propose that *Bidens aristosa* var. *retrorsa* be completely merged with *B. aristosa* proper. The morphology and nomenclature of this species would then be:

Bidens aristosa (Michx.) Britton, Bull. Torrey Bot. Club **20:** 281. 1893.

Achenes awned, the awns antrorsely barbed: forma **aristosa.**

Coreopsis aristosa Michx., Fl. Bor. Am. **2:** 140. 1803.
Coreopsis aristata Muhl. ex Willd., Sp. Pl. **3:** 2253. 1804.
Coreopsis aurea Lindl., Bot. Reg. *pl. 1228.* 1829.
Coreopsis involucrata Nutt., Jour. Acad. Phila. **7:** 74. 1834.
Diodonta involucrata (Nutt.) Nutt., Trans. Am. Phil. Soc. n.s. **7:** 361. 1841.
Diodonta aristosa (Michx.) Nutt., Trans. Am. Phil. Soc. n.s. **7:** 360. 1841.
Bidens involucrata (Nutt.) Britt., Bull. Torrey Bot. Club **20:** 281. 1893 (*non* Sch.-Bip., 1846, *nec* Phil., 1891).
Bidens polylepis Blake, Proc. Soc. Wash. **35:** 78. 1922.
Bidens polylepis Blake var. *typica* Sherff, Brittonia **6:** 339. 1948.
Bidens aristosa (Michx.) Britt. var. *retrorsa* (Sherff) Wunderlin forma *involucrata* (Nutt.) Wunderlin, Ann. Mo. Bot. Gard. **59:** 472. 1972.

Achenes awned, the awns retrorsely barbed: forma **fritcheyi** (Fern.) Wunderlin, Ann. Mo. Bot. Gard. **59:** 471. 1972.

Bidens aristosa (Michx.) Britt. var. *fritcheyi* Fern., Rhodora **15:** 78. 1913.
Bidens involucrata (Nutt.) Britt. var. *retrorsa* Sherff, Bot. Gaz. **76:** 160. 1923.
Bidens polylepis Blake var. *retrorsa* Sherff, Bot. Gaz. **80:** 386. 1925.
Bidens aristosa (Michx.) Britt. var. *retrorsa* (Sherff) Wunderlin, Ann. Mo. Bot. Gard. **59:** 472. 1972.

Achene awns absent or reduced to tiny stubs: forma **mutica** (Gray) Wunderlin, Ann. Mo. Bot. Gard. **59:** 471. 1972.

Coreopsis aristosa Michx. var. *mutica* Gray Man. Bot. ed. **5:** 260. 1867.
Bidens aristosa (Michx.) Britt. var. *mutica* (Gray) Gattinger ex Fern., Rhodora **15:** 78. 1913.

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B. L. L.
HERBARIUM
SOUTHERN METHODIST UNIVERSITY
DALLAS, TEXAS 75275

E. B. S.
DEPARTMENT OF BOTANY & BACTERIOLOGY
UNIVERSITY OF ARKANSAS
FAYETTEVILLE, ARKANSAS 72701

THE FLORA OF GARDINERS ISLAND

EDWARD J. HEHRE, JR.

In 1639, an island bearing the Indian name of Manchonake (Isle of Death) was deeded to Lion Gardiner by King Charles I of Great Britain. This deed is important historically as it represents the first manorial grant in the colonies; moreover, it was a British grant in the Dutch colonial settlement of New Amsterdam. Gardiners Island, as it is now called, has remained in the possession of the Gardiner family through an unprecedented sixteen generations. Today, this manor stands alone — the sole surviving member of a once select group of estates. Covering an area of about 3400 acres, Gardiners Island lies between the north and south forks of eastern Long Island, New York (Lat.: 41°03′ - 41°07′ N; Long.: 72°05′ - 72°08′ W). It is the geographic boundary between Gardiners Bay to the west (beyond which lies Shelter Island and the entrance to Peconic Bay) and Block Island Sound to the east (Figure 1).

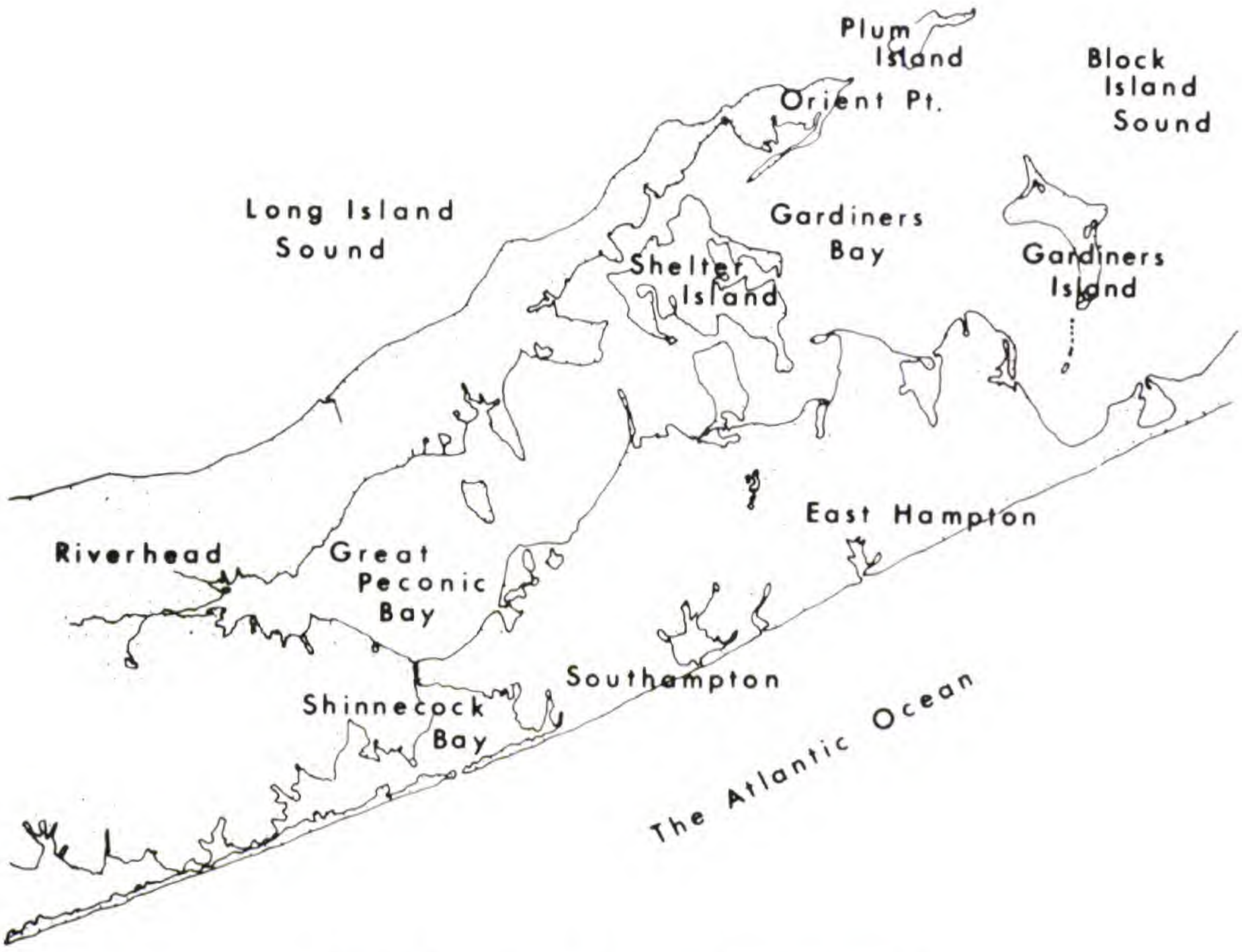

Figure 1. Map of eastern Long Island.

Gardiners Island is inhabited by only a few people, and its limited accessibility to the public has allowed much of the island to remain in its natural state. Although no rare or unusual species of plants have been found there, a large tract of virgin white oak, known as the Bostwick Forest, is without parallel in the Northeastern United States — a relict of the forests of pre-colonial Long Island. The island is a sanctuary for several species of birds, which are either absent or rare elsewhere on Long Island (e.g., Osprey, Oyster-catcher, American Egret, Wild Turkey, and Glossy Ibis). There also exists a large deer population, and while actual figures on its size are not known, the high browse-lines at the edges of woodlands plus the several individuals that die each winter indicate that the herd greatly exceeds the optimum number that the island can support.

Despite its long and interesting history, very little information about the plant life of Gardiners Island has been published. Burnham and Latham (1914–1925) compiled a checklist of the plants of Southold Town in which they included fifty-four taxa specifically from Gardiners Island.[1] Since their study was concerned primarily with Southold Town, their account of the plants of Gardiners Island merely represents several trips to the island and not a systematic study.

At present, 403 taxa have been recorded from Gardiners Island, including those listed by Burnham and Latham, Taylor (1922) and Peters (1973). Ten grow only in cultivation; 318 of the remaining 393 taxa are native; Appendix I includes all taxa recorded from the island. A checklist alone cannot do justice to the variety of interesting habitats encountered during this study. It seems appropriate, therefore, to describe the characteristic vegetation of these habitats, in an attempt to convey a more meaningful and more comprehensive picture of the flora of Gardiners Island. Voucher specimens are deposited in the Hodgdon Herbarium of the University of New Hampshire (NHA). With a few exceptions, the nomenclature used for angiosperms and gymnosperms follows that of *Gray's Manual of Botany* (8th ed., 1950). Nomenclature used for ferns follows Seymour (1969).

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[1]Gardiners Island lies south of the political boundary dividing the town of Southold on the North Fork and Easthampton on the South Fork. Thus, the island is part of Easthampton, not Southold.

Beaches. Although beaches extend around the entire perimeter of Gardiners Island, the largest and most well-developed ones are the barrier beaches associated with the major coastal ponds. Such broad expanses as those seen at Great Pond, Bostwick Creek and Tobaccolot Pond have a conspicuous flora typical of the beaches of eastern Long Island. *Ammophila breviligulata* (beachgrass) is the dominant component; other members of this community often include *Lathyrus japonicus* var. *glaber*, *L. japonicus* var. *pellitus* and, to a lesser extent, *Strophostyles helvola* and *Opuntia humifusa* (the latter was found only at Bostwick Creek).

Perhaps the most unusual beach association on the island occurs at Cherry Hill, where there is a coarse gravel and cobble beach at the base of cliffs composed of glacial till. These cliffs rise to a height of nearly 100 feet. Although most of the species found there occur elsewhere on Gardiners Island, it is only at Cherry Hill that they form a distinct plant association (e.g., *Glaucium flavum*, *Nepeta cataria*, *Plantago major* var. *scopulorum*, *Oenothera biennis*, *Verbascum thapsus*, and *Teucrium canadense*).

There are numerous species encountered on beaches; many are major components of the beach flora in areas from which *Ammophila* is absent (e.g., *Cyperus grayii*, *Artemisia stelleriana*, *Arenaria peploides* var. *robusta*, *Atriplex patula* var. *hastata*, *Cakile edentula*, *Salsola kali*, *Euphorbia polygonifolia*, *Mollugo verticillata*, *Suaeda linearis*, *Triplasis purpurea*, *Chenopodium botrys*, *C. glaucum*, *Polygonum glaucum*, *P. aviculare* var. *littorale*, and *Solidago sempervirens*).

The cliffs to which I alluded earlier are found only on the northern regions of the island. They extend from Crow Head to Home Pond along the western shore; on the east, they extend from Bostwick Creek to Tobaccolot Pond and are most prominent at Eastern Plain Point. (The highest point of land on Gardiners Island is Whale Hill on the northern shore of Eastern Plain Point. It is about 120 feet above sea level.) Due to the steep nature of the cliffs and the continual slumping of the unconsolidated glacial till, plants are abundant only locally, and there are but a few common species (e.g., *Solidago tenuifolia*, *Chrysopsis falcata*, *Lactuca scariola* f. *integrifolia*, *Erigeron pusillus*, *Gnaphalium obtusifolium*, *Equisetum arvense*, *Rumex acetosella*, *Cenchrus longispinus*, and *Plantago lanceolata*).

A discussion of shoreline vegetation on eastern Long Island would be incomplete without including *Phragmites communis* var. *berlandieri*. Although *Phragmites* is present on Gardiners Island, it certainly is not a conspicuous component of either the beach or marsh flora. It occurs sporadically, usually in small colonies on barrier beaches, parts of which are subject to occasional destruction during storms. Apparently, it colonizes open areas more readily than it competes with already existing vegetation. The only extensive colony of *Phragmites* on the island resulted directly from man's destruction of the original vegetation. Located adjacent to the boat basin in an area that was filled with dredge soil during construction of the harbor, rapid recolonization of the region by *Phragmites* led to the virtual exclusion of all other plants, reminiscent of a far-too-common sight along the shores and in the marshes of the South Fork of eastern Long Island.

Coastal Ponds with Salt Marshes. The salt marshes on Gardiners Island are among the finest tidal wetlands on eastern Long Island. They have remained undisturbed, having escaped the fate of the majority of our marshes (i.e., mosquito ditching, filling, and the subsequent invasion and replacement of vast segments by *Phragmites*). There are three large wetlands regions: Great Pond, at the southern tip of the island; Home Pond, the most extensive marsh with the greatest species diversity, located near the boat basin; and Cherry Hill Pond, at the extreme western point of the island.

Both Great Pond and Home Pond have permanent inlets into Gardiners Bay and thus support a diversified benthonic flora. Populations of marine algae predominate (e.g., *Cladophora* spp., *Enteromorpha* spp., *Codium fragile* ssp. *tomentosoides, Gracilaria foliifera, Polysiphonia harveyi*); the submergent angiosperm components are *Zostera marina* var. *stenophylla* and *Ruppia maritima* var. *longipes*. On Gardiners Island, *Zostera* is limited to small isolated patches in Great Pond. Large colonies of *Zostera* are very common, however, in Gardiners Bay and throughout Peconic Bay. *Ruppia*, on the other hand, is abundant in all coastal ponds on the island but, unlike *Zostera*, is not found beyond confined coastal ponds on eastern Long Island.

Cherry Hill Pond is permanently closed by a barrier beach (i.e., there is no inlet). Salinity readings of 30 $^{o}/_{oo}$ (ppt), how-

ever, indicate a continual inundation of seawater over the low barrier beach. The dominant benthonic flora consists of *Cladophora* spp. and *Ruppia*.

The lower limit of the marshes is typically a zone of *Spartina alterniflora* with distinct zones of *S. patens* and *Distichlis spicata* occurring at slightly higher elevations. A narrow band of *Juncus gerardi* is present near the high water line. *Baccharis halimifolia* and *Iva frutescens* var. *oraria* are the major components of a dense shrub zone at and above the high water line at Great Pond and Home Pond. They have not been observed at Cherry Hill Pond, where this zone is dominated chiefly by *Myrica pensylvanica*.

There are several additional species that occur as common components of the salt marshes on Gardiners Island (e.g., *Salicornia europaea, S. bigelovii, S. virginica, Plantago oliganthos, Gerardia maritima, Pluchea purpurascens* var. *succulenta, Solidago sempervirens, Scirpus americanus, S. robustus, Limonium carolinianum,* and *Hibiscus palustris*). Some are found in all of the marshes on the island; others are more restricted in their distribution.

Additional wetlands surround three small ponds between the boat basin and Great Pond (Airport Pond, Gales Pond, Little Pond). They are completely contained by barrier beaches but are inundated regularly at high water. Salinities are generally in the range of 29–31 $^{o}/_{oo}$ near the beaches, dropping sharply to less than 5 $^{o}/_{oo}$ along the eastern shores where there are numerous freshwater springs. These areas of lower salinity support large stands of *Typha latifolia* and *Hibiscus palustris*. The dominant salt marsh grass is *Spartina alterniflora*.

In addition to ponds with well-developed salt marshes, there are two other coastal ponds, Bostwick Creek and Tobaccolot Pond. Neither has a permanent inlet although sea water inundates both, particularly during storms.

Bostwick Creek. Bostwick Creek is located at the northern end of the island. It was open to Gardiners Bay through a large inlet until 1967, when it was closed during a severe storm. Although it has remained closed since that time, the pond is inundated periodically (during extreme high tides and storms) over

the low barrier beach on its eastern shore. The salinity in Bostwick Creek remains a relatively constant 10–12 °/oo.

The submergent vegetation consists mainly of *Ruppia maritima* var. *longipes* and the euryhaline green alga, *Enteromorpha intestinalis*. Along the shoreline, there are isolated patches of *Spartina alterniflora, S. patens,* and *Pluchea,* indicative of a once prevalent salt marsh.

There are two streams which empty into Bostwick Creek from the Bostwick Forest. They create marshy freshwater cul-de-sacs where one finds large stands of *Typha latifolia* and *Thelypteris palustris* var. *pubescens*. Other plants found in these freshwater regions of the pond include *Elatine minima* and *Sagittaria latifolia*. Overall, there are several species comprising the shoreline vegetation of Bostwick Creek (e.g., *Ptilimnium capillaceum, Teucrium canadense, Amorpha fruticosa, Galium palustre, Eleocharis acicularis, E. olivacea, Hibiscus palustris, Cyperus strigosus, C. grayii, C. diandrus,* and *C. filicinus*).

Tobaccolot Pond. Tobaccolot Pond is located on the eastern shore of Gardiners Island south of Eastern Plain Point. The original name was Tobacco Lot, signifying the area where tobacco was grown by the Indians prior to 1639. There is a deep channel at the northern end of the pond; it is at this point that a narrow section of barrier beach is often broken through during storms, allowing salt water into the pond. The prinicpal freshwater sources are numerous springs and a single stream, Willow Brook. The combination of infrequent salt water intrusion, poor mixing when inundation does occur and the large volume of fresh water supplied to the pond accounts for its relatively low salinity (about 4 °/oo).

The submergent vascular flora found here is slightly more diversified than in those ponds with higher salinities (e.g., *Ludwigia palustris* var. *americana, Potamogeton perfoliatus* var. *bupleuroides, P. pusillus* var. *tenuissimus, Elatine minima, Ruppia maritima* var. *longipes*). As in Bostwick Creek, there are marshy cul-de-sacs created by springs with large stands of *Typha latifolia* and *Thelypteris palustris* var. *pubescens*. Other conspicuous members of this community not seen at Bostwick Creek include *Scirpus cyperinus, Gratiola aurea* and *Lemna minor*.

A few of the shoreline plants found at Tobaccolot are widespread on the island (e.g., *Pluchea, Ptilimnium, Cyperus strigosus, C. grayii,* and *C. filicinus*). The dominant vegetation, however, is unique, with several species restricted to this locality (e.g., *Sesuvium maritimum, Rumex maritimus* var. *fueginus, Lechea maritima, Juncus militaris, Hypericum boreale, Euphorbia supina,* and *Gnaphalium uliginosum*). In addition to these plants, the upper border of Tobaccolot Pond supports the largest stand of *Hibiscus palustris* on the island. It extends completely around the perimeter of the pond and provides a spectacular display of color in late summer, when the plants are in full bloom. The pink-flowered *H. palustris* var. *palustris* is the more abundant form; there are a few patches of the white-flowered *H. palustris* var. *peckii* at the northwest end of the pond. This form was observed in only one other region on the island, at Little Pond.

The vegetation at the extreme southern end of Tobaccolot Pond was not examined due to the presence of a large Osprey colony. Several attempts were made to reach this area and each was met with strenuous vocal disapproval on the part of the inhabitants. Rather than incite additional anger and possible attack, the author thought it best to retreat.

Freshwater Ponds and Streams. Gardiners Island is replete with small ponds, marshy swales, springs, and a few streams. Since these regions are numerous, descriptions will include only the largest and most significant.

Garlick Pond. Garlick Pond[2] is situated near the boat basin, between the two roads leading from the harbor to the kennels and barns. It is shallow and muddy, with a conduit allowing for drainage into the harbor. The pond is named for Goodie (Goodwife) Garlick, the first woman accused of witchcraft on Long Island. She was tried for this crime in Connecticut in 1658. Released for lack of evidence, she came in the same year, by invitation from Lion Gardiner, to live on Gardiners Island near the pond which now bears her name. (In view of the origin of the name "Garlick" Pond, it is interesting that one finds field garlic, *Allium vineale,* growing along the banks of this pond

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[2]Garlick Pond is also called Gaylor Hole on topographic maps.

and nowhere else on the island. It is conceivable, even probable, that Goodie Garlick was responsible for introducing this European plant to her home on Gardiners Island in the seventeenth century.)

Much of the shoreline of Garlick Pond is impenetrable, with dense populations of *Panicum clandestinum* and *Rubus frondosus*. There are only two areas of the pond that are accessible. 1) Large colonies of *Heracleum maximum* and *Scrophularia lanceolata* are found along the southwestern shore. Isolated clumps of *Iris versicolor* grow in shallow water near the shore, while the aforementioned *Allium vineale* occurs along the one open section of the pond border. 2) The northern section of the pond is marshy but can be reached, albeit with some difficulty. There are several interesting plants found here (e.g., *Echinochloa walteri, Impatiens capensis, Leersia oryzoides, Scirpus cyperinus* var. *pelius* f. *condensatus,* and *Eleocharis obtusa*). The vegetation on the western shore consists of a dense stand of *Hibiscus palustris,* which also occurs in tussocks throughout the pond.

Bostwick Dam. Bostwick Dam is a small pond created by a dam at the mouth of Upper Willow Brook, and one of the large cul-de-sacs in Bostwick Creek is fed by the outfall from this pond. The pond is accessible by a road through the Bostwick Forest, which passes over the dam. There is a dense shrub zone comprising the major shoreline vegetation (e.g., *Myrica pensylvanica, Ilex verticillata, Cephalanthus occidentalis*). There are very few submergent species; the common ones include *Elatine minima* and *Potamogeton pusillus* var. *tenuissimus.* A further note regarding Bostwick Dam: it is perhaps the largest Black-crowned Night Heron rookery on the island.

Canoe Place. Canoe Place is the major stream which flows through the Bostwick Forest. Like all the bodies of fresh water on Gardiners Island, it is spring-fed. This stream empties into Bostwick Creek, forming a broad expanse of marsh (the *Typha-Thelypteris* association previously mentioned).

Only two species (*Chrysosplenium americanum* and *Cardamine pensylvanica*) have been found growing partially or totally submerged in the stream, while the swampy borders provide for a diverse flora (e.g., *Acer rubrum, Nyssa sylvatica, Viola mack-*

loskyii ssp. *pallens, V. cucullata, Veratrum viride, Symplocarpus foetidus, Ranunculus repens, Polygonum sagittatum, P. arifolium* var. *pubescens, Hypericum mutilum, Onoclea sensibilis, Osmunda cinnamomea, Thelypteris novaboracensis, Triodia flava, Carex crinita* var. *brevicrinus, Lycopus virginicus,* and *Boehmeria cylindrica*).

Wolfies Hole and Willow Brook. Wolfies Hole is a large kettle pond northwest of Whale Hill. It is the largest inland pond on the island and provides the source for Willow Brook, which flows into Tobaccolot Pond. A thicket of *Decodon verticillata* creates an impenetrable barrier along most of the eastern shore. The remainder of the pond border is open, with dense stands of *Typha latifolia* and occasional clumps of *Osmunda regalis* var. *spectabilis* the most conspicuous plants along the muddy shores.

The floating and submergent vegetation in Wolfies Hole is sparse, although there are localized areas within the pond where aquatic plants are abundant (e.g., *Lemna minor, Spirodela polyrhiza, Myriophyllum humile* f. *capillaceum, Potamogeton diversifolius* var. *trichophyllus*). Other conspicuous plants consist of a few species of emergent aquatics (e.g., *Carex lurida, Juncus acuminatus, J. effusus* var. *solutus,* and *Eleocharis smallii*). There is a single large tree of *Liriodendron tulipifera* growing at the edge of the pond. As this is the only tulip tree on Gardiners Island, and as there is no indication that it was planted here, it may be the lone surviving member of a native species that has virtually disappeared from eastern Long Island.

Willow Brook is an intermittent stream that is little more than a muddy ditch during the summer. However, a dam constructed at the mouth of the stream as it enters Tobaccolot Pond has created a small pond and marsh. Among the several species of plants found along Willow Brook, the most common are *Myosotis laxa* and eight species of *Carex*. The marshy section of the pond is almost exclusively a mixture of *Rumex verticillata* and *Scirpus cyperinus*. Aquatic vegetation is sparse, although there is one colony of *Pontederia cordata* covering a large area near the dam. Other aquatic plants include *Lemna, Spirodela, Najas flexilis* and *Potamogeton pusillus* var. *tenuissimus*. The dominant shoreline plant is *Decodon verticillata*.

Below the dam, along the swampy western border of Tobac-

colot Pond, there is a thicket of *Alnus serrulata* f. *novaboracensis* and a few large trees of *Salix nigra*; neither of the two species has been seen elsewhere on the island. Other common plants in this region include *Bidens cernua* and *Myosotis laxa.*

Casey Pond. Casey Pond is a small kettlehole at the western edge of Rogers Woods. There are a few species of aquatic plants found only in this pond (e.g., *Proserpinaca palustris, Callitriche verna, Hypericum boreale* f. *callitrichoides*). The dominant emergent aquatic plant is *Juncus effusus* var. *costulatus*; there are also several patches of *Eleocharis tenuis.*

Bostwick Forest. The Bostwick Forest extends over most of the northern sector of Gardiners Island; it is a large tract of virgin timber whose principal components include *Quercus alba, Q. velutina, Carya ovalis* and *C. glabra.* The white oak (*Q. alba*) is the most common tree in the Bostwick Forest. It also attains the greatest size; many are close to 100 feet in height and the largest one has a d.b.h. of over five feet. There are several other species of trees comprising minor constituents of the forest (e.g., *Carya tomentosa, Quercus marilandica, Betula lenta, B. populifolia, Ostrya virginiana, Cornus florida,* and *Fagus grandifolia*).

The forest borders above the salt marsh at Home Pond are characterized by *Quercus stellata* and *Nyssa sylvatica. Nyssa* is also found in swampy regions of the Bostwick Forest with *Acer rubrum.* Two species of trees rarely seen outside of cultivation on eastern Long Island can be found along roads in the forest. Young seedlings of both *Paulownia tomentosa* and *Acer pseudoplatanus* indicate successful naturalization.

There is an obvious absence of young oak seedlings in the Bostwick Forest. The primary reason for their absence is equally obvious: the dominant understory vegetation consists of *Smilax rotundifolia,* whose dense stands, six feet or more in height, extend throughout the forest. *Smilax* allows for little else to grow and renders most of the forest impenetrable. It is also an actively climbing plant and, with *Toxicodendron radicans,* often forms a dense canopy over the tallest trees.

Vitis labrusca, another plant which quickly colonizes open areas, is more restricted in its distribution within the forest than *Smilax.* It is found primarily (but not exclusively) about the open borders

of the woods. This does not imply that *Smilax* is more abundant than *Vitis* on Gardiners Island. There are dense colonies of *Vitis* over many regions of the island; *Smilax*, although not restricted to the Bostwick Forest, grows most abundantly there. *Vitis* is also capable of overtopping large trees (it is occasionally seen encroaching on the forest trees) but it seems to thrive where the vegetation is low and shrubby.

The large populations of *Smilax rotundifolia* and *Vitis labrusca* have eliminated most other understory vegetation from a large portion of the Bostwick Forest. A few species of small trees and shrubs are present in limited numbers (e.g., *Celastrus orbiculatus, Crataegus crus-galli, Lindera benzoin, Sassafras albidum, Gaylussacia baccata, Vaccinium corymbosum, V. angustifolium* var. *laevifolium, Rhus typhina, Viburnum recognitum,* and *Sambucus canadensis*). For the same reason, very few herbaceous plants grow in the Bostwick Forest; many of those that do are found along the roadways (e.g., *Poa pratensis, Aster* spp., *Rubus frondosus, R. phoenicolasius, Asclepias purpurascens, Solidago rugosa, Tovara virginiana, Geranium maculatum*). One exception is a large glade near Canoe Place where there is a dense stand of *Thelypteris novaboracensis* and *Triodia flava.*

Rogers Woods. Rogers Woods extends from the Airport Road south of the boat basin, eastward to the western shore of Tobaccolot Pond. It is essentially a young oak-hickory woods (e.g., *Quercus alba, Q. velutina, Carya glabra,* and *C. ovalis*). Some of the other trees and shrubs found in this region include *Acer rubrum, Celtis occidentalis, Hamamelis virginiana* and *Amelanchier laevis. Smilax rotundifolia* is a common understory plant in dry areas, but it is not as dense nor as extensive as in the Bostwick Forest.

A large part of this wooded area consists of swales, which are usually muddy and occasionally have standing water. *Acer rubrum* is the most common tree in these wet swales; the one small grove of *Hamamelis* seen on the island also seems to prefer this habitat. On the western edge of Rogers Woods, in areas of standing water and on muddy shores, a few unusual plants occur in large numbers (e.g., *Hottonia inflata, Riccia fluitans* and *Ricciocarpus natans*). The most common trees around the perimeter of this woods are *Prunus serotina* and *Robinia pseudo-acacia.* There is a small stand of young *Ailanthus altissima* at one edge of the woods; this species was not seen elsewhere on the island.

Fields and Roads. There are several hundred acres of fields on Gardiners Island. Most of this land was cultivated during colonial times when the island was a self-sustaining community. The most extensive fields occur on the southern half of the island between Home Pond and Great Pond, but they are also prevalent in the vicinity of Cherry Hill. Many are mowed on a regular basis, thereby maintaining the grassland condition. Those that are not mowed show a secondary invasion of shrubs and small trees.

There are several common species of grasses in these field communities (e.g., *Andropogon scoparius, Echinochloa crusgalli, Holcus lanatus, Paspalum laeve* var. *pilosum, Poa pratensis, Setaria glauca,* and *Vulpia octoflora* var. *tenella*). Some are restricted to one or two localities, while others are more widespread and occur in most fields on the island.

There are several other herbaceous plants common in the fields on Gardiners Island. The following list includes only those that are most conspicuous:

Achillea millefolium
Asclepias syriaca
A. tuberosa
Chrysanthemum leucanthemum var. *pinnatifidum*
Cirsium altissimum
C. discolor
C. horridulum
C. pumilum
Eupatorium hyssopifolium
Hypericum perforatum
Linaria vulgaris
Onopordum acanthium
Ornithogalum nutans
Potentilla canadensis
Pycnanthemum muticum
P. tenuifolium
Ranunculus bulbosus
Rubus enslenii
Rudbeckia hirta
Satureja vulgaris var. *neogaea*
Sisyrinchium atlanticum
S. montanum var. *crebrum*
Solanum caroliniense
Trifolium pratense
Veronica serpyllifolia
V. tenella

In addition, a few plants of *Habenaria lacera* were seen in a field near the boat basin. This is the only orchid encountered on Gardiners Island during this study, although two other species (*Habenaria psychodes* and *H. clavellata*) were reported by Burnham and Latham (1917). These colonies have not as yet been rediscovered.

In fields where secondary succession has been allowed to proceed normally, one finds several species of woody plants (e.g., *Myrica pensylvanica, Rhus copallina, Prunus maritima, P. serotina, Rosa eglanteria, R. virginiana, Vitis labrusca,* and *Robinia pseudo-acacia*). *Robinia* and *Prunus serotina* are the most common woody plants along stone walls and roadsides.

There are numerous roadside weeds on the island. Some are conspicuous members of other associations, particularly fields; others are common only along the many dirt roads that traverse the island (e.g., *Taraxacum officinale, Plantago aristata, P. lanceolata, Cichorum intybus, Eragrostis cilianensis, E. pectinacea, Helenium flexuosum, Juncus greenei, J. tenuis, Matricaria matricarioides, Linaria canadensis, Trifolium repens,* and *Panicum oligosanthes* var. *scribnerianum*).

Other Notes on the Vegetation. Aside from a few small and inconspicuous plants of *Juniperus communis* and *J. virginiana,* there are no members of the Coniferales growing outside of cultivation on Gardiners Island. There are a few large trees of *Pinus strobus* planted at the southwest edge of the Bostwick Forest; a single tree of *Larix kaempferi* grows in the cemetery; and there are large stands of *Picea pungens* and *Pinus resinosa* south of the boat basin on the western shore, which were planted in the 1930's.

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35 MAIN STREET
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APPENDIX I. ANNOTATED CHECKLIST

Equisetaceae

1. *Equisetum arvense* L.

Osmundaceae

2. *Osmunda cinnamomea* L.
3. *O. regalis* L. var. *spectabilis* (Willd.) Gray

Polypodiaceae

4. *Dryopteris spinulosa* (O. F. Muell.) Watt
5. *Onoclea sensibilis* L.
6. [1]*Thelypteris hexagonoptera* (Michx.) Weather.
7. *T. novaboracensis* (L.) Nieuwl.
8. *T. palustris* (Salisbury) Schott var. *pubescens* (Lawson) Fern.
9. *T. simulata* (Davenp.) Nieuwl.
10. *Woodwardia areolata* (L.) Moore

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[1]Burnham & Latham records; not observed in this study.
[2]Introduced.
[3]In cultivation only.
[4]Burnham & Latham records; also observed in this study.
[5]Recorded by Taylor; not observed in this study.

Pinaceae

[2,3] *Larix kaempferi* Sarg.
[3] *Picea pungens* Engelm.
[3] *Pinus resinosa* Ait.
[3] *P. strobus* L.

Cupressaceae

11. *Juniperus communis* L.
12. *J. virginiana* L.

Typhaceae

13. *Typha angustifolia* L.
14. *T. latifolia* L.

Sparganiaceae

15. [1] *Sparganium androcladum* (Engelm.) Morong
16. [1] *S. eurycarpum* Engelm.

Zosteraceae

17. [4] *Potamogeton diversifolius* Raf. var. *trichophyllus* Morong
18. *P. perfoliatus* L. var. *bupleuroides* (Fern.) Farw.
19. *P. pusillus* L. var. *tenuissimus* Mert. & Koch
20. *Ruppia maritima* L. var. *longipes* Hagstr.
21. [1] *Zannichellia palustris* L.
22. *Zostera marina* L. var. *stenophylla* Aschers. & Graebn.

Najadaceae

23. *Najas flexilis* (Willd.) Rostk. & Schmidt

Alismataceae

24. *Sagittaria latifolia* Willd.

Gramineae

FESTUCEAE

25. [2] *Bromus tectorum* L.
26. [2] *Dactylis glomerata* L. var. *ciliata* Peterm.
27. [2] *D. glomerata* L. var. *detonsa* Fries
28. *Distichlis spicata* (L.) Greene
29. [2] *Eragrostis cilianensis* (All.) Mosher
30. *E. pectinacea* (Michx.) Nees
31. *E. spectabilis* (Pursh) Steud. var. *sparsihirsuta* Farw.
32. *Festuca rubra* L.
33. *Glyceria striata* (Lam.) Hitchc.
34. *Phragmites communis* Trin. var. *berlandieri* (Fourn.) Fern.
35. [2] *Poa compressa* L.
36. *P. pratensis* L.
37. *Triodia flava* (L.) Smythe
38. *Triplasis purpurea* (Walt.) Chapm.
39. *Vulpia octoflora* (Walt.) Rydb. var. *tenella* (Willd.) Fern.

Gramineae (continued)

HORDEAE

40. *Agropyron repens* (L.) Beauv.
41. [4]*Elymus villosus* Muhl.
42. *E. virginicus* L. var. *jejunus* (Ramaley) Bush

AVENEAE

43. [2]*Holcus lanatus* L.

AGROSTIDEAE

44. *Agrostis stolonifera* L. var. *palustris* (Huds.) Farw.
45. *A. hyemalis* (Walt.) BSP.
46. *A. scabra* Willd.
47. *Ammophila breviligulata* Fern.
48. [1]*Aristida purpurascens* Poir.
49. [2]*Phleum pratense* L.

CHLORIDEAE

50. *Spartina alterniflora* Loisel.
51. *S.* × *caespitosa* A. A. Eat.
52. *S. patens* (Ait.) Muhl.
53. *S. pectinata* Link

PHALARIDEAE

54. [2]*Anthoxanthum odoratum* L.

ORYZEAE

55. *Leersia oryzoides* (L.) Sw.

PANICEAE

56. *Cenchrus longispinus* (Hack.) Fern.
57. [2]*Digitaria sanguinalis* (L.) Scop.
58. [2]*Echinochloa crusgalli* (L.) Beauv.
59. *E. walteri* (Pursh) Nash
60. *Panicum capillare* L.
61. *P. clandestinum* L.
62. *P. lanuginosum* Ell. var. *fasciculatum* (Torr.) Fern.
63. *P. lanuginosum* Ell. var. *septentrionale* Fern.
64. *P. oligosanthes* Schultes var. *scribnerianum* (Nash) Fern.
65. *P. virgatum* L. var. *spissum* Linder
66. *Paspalum laeve* Michx. var. *pilosum* Scribn.
67. [2]*Setaria glauca* (L.) Beauv.

ANDROPOGONEAE

68. *Andropogon gerardi* Vitman
69. *A. scoparius* Michx.

MAYDEAE

70. *Tripsacum dactyloides* L.

Cyperaceae

71. *Bulbostylis capillaris* (L.) C. B. Clarke
72. *Carex annectens* Bickn.
73. *C. canescens* L.
74. *C. crinita* Lam. var. *brevicrinus* Fern.
75. *C. cristatella* Britt.
76. *C. debilis* Michx.
77. *C. digitalis* Willd.
78. *C. hormathodes* Fern.
79. *C. laevivaginata* (Kukenth.) Mackenz.
80. *C. lurida* Wahlenb.
81. *C. muhlenbergii* Schkuhr
82. [1]*C. retroflexa* Muhl.
83. *C. scoparia* Schkuhr
84. *C. stipata* Muhl.
85. *C. swanii* (Fern.) Mackenz.

Cyperaceae (continued)

86. *C. vulpinoidea* Michx.
87. *Cyperus diandrus* Torr.
88. *C. filicinus* Vahl
89. *C. filiculmis* Vahl var. *macilentus* Fern.
90. *C. grayii* Torr.
91. *C. strigosus* L.
92. [4]*Eleocharis acicularis* (L.) R. & S.
93. *E. obtusa* (Willd.) Schultes
94. *E. olivacea* Torr.
95. *E. smallii* Britt.
96. *E. tenuis* (Willd.) Schultes
97. *Scirpus americanus* Pers.
98. *S. cyperinus* (L.) Kunth
99. *S. cyperinus* (L.) Kunth var. *pelius* Fern. f. *condensatus* (Fern.) S. F. Blake
100. *S. robustus* Pursh

Araceae

101. *Arisaema triphyllum* (L.) Schott
102. *Symplocarpus foetidus* (L.) Nutt.

Lemnaceae

103. *Lemna minor* L.
104. *Spirodela polyrhiza* (L.) Schleid.

Pontederiaceae

105. *Pontederia cordata* L.

Juncaceae

106. *Juncus acuminatus* Michx.
107. *J. brevicaudatus* (Engelm.) Fern.

108. *J. effusus* L. var. *costulatus* Fern.
109. *J. effusus* L. var. *solutus* Fern. & Wieg.
110. *J. gerardi* Loisel.
111. *J. greenei* Oakes
112. *J. militaris* Bigel.
113. [4]*J. tenuis* Willd.

Liliaceae

114. [2]*Allium vineale* L.
115. [2]*Asparagus officinalis* L.
116. *Maianthemum canadense* Desf.
117. [2]*Ornithogalum nutans* L.
118. *Smilax rotundifolia* L.
119. *Uvularia sessilifolia* L.
120. [4]*Veratrum viride* Ait.
121. *Yucca filamentosa* L.

Dioscoreaceae

122. [1]*Dioscorea villosa* L.

Iridaceae

123. *Iris versicolor* L.
124. *Sisyrinchium atlanticum* Bickn.
125. *S. montanum* Greene var. *crebrum* Fern.

Orchidaceae

126. [1]*Habenaria clavellata* (Michx.) Spreng.
127. *H. lacera* (Michx.) Lodd.
128. [1]*H. psychodes* (L.) Spreng.

Salicaceae

129. *Salix nigra* Marsh.

Myricaceae

130. *Myrica pensylvanica* Loisel.

Juglandaceae

131. *Carya glabra* (Mill.) Sweet
132. *C. ovalis* (Wang.) Sarg.
133. [1]*C. ovata* (Mill.) K. Koch
134. *C. tomentosa* Nutt.
[3]*Juglans nigra* L.

Corylaceae

135. *Alnus serrulata* (Ait.) Willd. f. *novaboracensis* (Britt.) Fern.
136. [5]*Betula allegheniensis* Britt.
137. *B. lenta* L.
138. [5]*B. nigra* L.
139. *B. populifolia* Marsh.
140. *Ostrya virginiana* (Mill.) K. Koch

Fagaceae

141. *Fagus grandifolia* Ehrh.
[2,3]*F. sylvatica* L. var. *purpurea* Ait.
142. *Quercus alba* L.
143. *Q. marilandica* Muenchh.
144. *Q. stellata* Wang.
145. *Q. velutina* Lam.

Ulmaceae

146. [4]*Celtis occidentalis* L.
147. [1]*Ulmus americana* L.
[2,3]*U. procera* Salisb.

Moraceae

148. [1]*Morus rubra* L.

Urticaceae

149. *Boehmeria cylindrica* (L.) Sw.
150. *Pilea pumila* (L.) Gray
151. [1,2]*Urtica urens* L.

Polygonaceae

152. *Polygonella articulata* (L.) Meisn.
153. *Polygonum arifolium* L. var. *pubescens* (Keller) Fern.
154. *P. aviculare* L. var. *littorale* (Link) W. D. J. Koch
155. [2]*P. convolvulus* L.
156. [2]*P. dubium* Stein
157. [4]*P. glaucum* Nutt.
158. *P. hydropiper* L.
159. *P. lapathifolium* L.
160. *P. pensylvanicum* L.
161. [4]*P. sagittatum* L.
162. [2]*Rumex acetosella* L.
163. *R. maritimus* L. var. *fueginus* (Phil.) Dusen
164. *R. orbiculatus* Gray
165. *R. verticillatus* L.
166. [4]*Tovara virginiana* (L.) Raf.

Chenopodiaceae

167. *Atriplex patula* L. var. *hastata* (L.) Gray
168. [2]*Chenopodium ambrosioides* L.
169. [2]*C. botrys* L.
170. [2]*C. glaucum* L.
171. [2]*C. lanceolatum* Muhl.
172. *Salicornia bigelovii* Torr.
173. *S. europaea* L.
174. *S. virginica* L.
175. *Salsola kali* L.
176. *Suaeda linearis* (Ell.) Moq.

Amaranthaceae

177. [2]*Amaranthus retroflexus* L.

Phytolaccaceae

178. *Phytolacca americana* L.

Aizoaceae

179. [2]*Mollugo verticillata* L.
180. [4]*Sesuvium maritimum* (Walt.) BSP.

Portulacaceae

181 [2]*Portulaca oleracea* L.

Caryophyllaceae

182. *Arenaria peploides* L. var. *robusta* Fern.
183. [2]*Cerastium vulgatum* L.
184. [2]*Dianthus armeria* L.
185. [2]*Silene cucubalus* Wibel
186. *Spergularia marina* (L.) Griseb.

Ranunculaceae

187. [2]*Ranunculus bulbosus* L.
188. [2,4]*R. repens* L.

Berberidaceae

189. [2]*Berberis thunbergii* DC.
190. [2]*B. vulgaris* L.

Magnoliaceae

191. *Liriodendron tulipifera* L.

Lauraceae

192. [4]*Lindera benzoin* (L.) Blume
193. *Sassafras albidum* (Nutt.) Nees

Papaveraceae

194. [2,4]*Glaucium flavum* Crantz

Cruciferae

195. [2]*Brassica nigra* (L.) Koch
196. *Cakile edentula* (Bigel.) Hook.
197. [2]*Capsella bursa-pastoris* (L.) Medic.
198. *Cardamine pensylvanica* Muhl.
199. *Lepidium virginicum* L.

Saxifragaceae

200. [4]*Chrysosplenium americanum* Schwein.

Hamamelidaceae

201. [4]*Hamamelis virginiana* L.

Platanaceae

[3]*Platanus occidentalis* L.

Rosaceae

POMEAE

202. *Amelanchier laevis* Wieg.
203. [1]*Crataegus arnoldiana* Sarg.
204. *C. crus-galli* L.
205. [1]*C. intricata* Lange
206. *C. macrosperma* Ashe
207. [2]*Pyrus communis* L.

POTENTILLEAE

208. *Fragaria virginiana* Duchesne
209. *Geum canadense* Jacq. var. *camporum* (Rydb.) Fern. & Weather.
210. [1]*Potentilla anserina* L.
211. *P. anserina* L. var. *groenlandica* Tratt.
212. *P. canadensis* L.
213. [2]*P. recta* L.

RUBEAE

214. [2]*Rubus phoenicolasius* Maxim.
215. *R. enslenii* Tratt.
216. *R. frondosus* Bigel.

POTERIEAE

217. *Agrimonia gyrosepala* Wallr.

ROSEAE

218. [2]*Rosa eglanteria* L.
219. [2]*R. multiflora* Thunb.
220. [2]*R. rugosa* Thunb.
221. *R. virginiana* Mill.

PRUNEAE

222. [4]*Prunus maritima* Marsh.
223. *P. serotina* Ehrh.

Leguminosae

224. *Amorpha fruticosa* L.
225. *Amphicarpa bracteata* (L.) Fern.
226. [1]*Desmodium canescens* (L.) DC.
227. *Lathyrus japonicus* Willd. var. *glaber* (Ser.) Fern.
228. *L. japonicus* Willd. var. *pellitus* Fern.
229. [2]*Lotus corniculatus* L.
230. *Robinia pseudo-acacia* L.
231. *Strophostyles helvola* (L.) Ell.
232. [2]*Trifolium arvense* L.
233. [2]*T. pratense* L.
234. [2]*T. procumbens* L.
235. [2]*T. repens* L.

Oxalidaceae

236. [2]*Oxalis corniculata* L.
237. *O. europaea* Jord.

Geraniaceae

238. *Geranium maculatum* L.

Simaroubaceae

239. [2]*Ailanthus altissima* (Mill.) Swingle

Polygalaceae

240. [4]*Polygala verticillata* L. var. *ambigua* (Nutt.) Wood

Euphorbiaceae

241. *Euphorbia polygonifolia* L.
242. *E. supina* Raf.

Callitrichaceae

243. *Callitriche verna* L.

Anacardiaceae

244. *Rhus copallina* L.
245. *R. glabra* L.
246. *R. typhina* L.
247. *Toxicodendron radicans* (L.) Kuntze

Aquifoliaceae

248. *Ilex verticillata* (L.) Gray

Celastraceae

249. [2]*Celastrus orbiculatus* Thunb.

Aceraceae

250. [2]*Acer pseudoplatanus* L.
251. [4]*A. rubrum* L.

Hippocastanaceae

[2,3]*Aesculus hippocastanum* L.

Balsaminaceae

252. [4]*Impatiens capensis* Meerb.

Vitaceae

253. *Parthenocissus vitacea* (Knerr) Hitchc.
254. *Vitis labrusca* L.

Malvaceae

255. *Hibiscus palustris* L.
256. *H. palustris* L. f. *peckii* House
[2,3]*H. syriacus* L.

Guttiferae

257. *Hypericum boreale* (Britt.) Bickn.
258. *H. boreale* (Britt.) Bickn. f. *callitrichoides* Fassett
259. *H. gentianoides* (L.) BSP.
260. *H. mutilum* L.
261. [2]*H. perforatum* L.
262. *H. virginicum* L.

Elatinaceae

263. *Elatine minima* (Nutt.) Fisch. & Mey.

Cistaceae

264. [4]*Hudsonia tomentosa* Nutt.
265. *Lechea maritima* Leggett

Violaceae

266. *Viola cucullata* Ait.
267. *V. fimbriatula* Sm.
268. *V. macloskyi* Lloyd ssp. *pallens* (Banks) Baker

Cactaceae

269. *Opuntia humifusa* Raf.

Lythraceae

270. *Decodon verticillatus* (L.) Ell.

Nyssaceae

271. *Nyssa sylvatica* Marsh.

Onagraceae

272. *Circaea quadrisulcata* (Maxim.) Franch. & Sav. var. *canadensis* (L.) Hara
273. *Epilobium coloratum* Biehler
274. *Ludwigia palustris* (L.) Ell. var. *americana* (DC.) Fern. & Grisc.
275. *Oenothera biennis* L.

Haloragaceae

276. [1]*Myriophyllum humile* (Raf.) Morong
277. *M. humile* (Raf.) Morong f. *capillaceum* (Torr.) Fern.
278. *Proserpinaca palustris* L.

Umbelliferae

279. [2]*Daucus carota* L.
280. *Heracleum maximum* Bartr.
281. *Ptilimnium capillaceum* (Michx.) Raf.
282. *Sanicula canadensis* L.

Cornaceae

283. [1]*Cornus alternifolia* L. f.
284. *C. florida* L.

Clethraceae

285. *Clethra alnifolia* L.

Ericaceae

286. *Gaylussacia baccata* (Wang.) K. Koch.
287. *Vaccinium angustifolium* Ait. var. *laevifolium* House
288. *V. atrococcum* (Gray) Heller
289. *V. corymbosum* L.

Primulaceae

290. [2]*Anagallis arvensis* L.
291. *Hottonia inflata* Ell.
292. [1]*Lysimachia ciliata* L.

Plumbaginaceae

292. *Limonium carolinianum* (Walt.) Britt.

Asclepiadaceae

294. *Asclepias incarnata* L. var. *pulchra* (Ehrh.) Pers.
295. [4]*A. purpurascens* L.
296. *A. syriaca* L.
297. *A. tuberosa* L.

Convolvulaceae

298. *Convolvulus sepium* L.
299. *Cuscuta gronovii* Willd.

Boraginaceae

300. [4]*Hackelia virginiana* (L.) I. M. Johnston
301. [4]*Myosotis laxa* Lehm.

Verbenaceae

302. *Verbena hastata* L.

Labiatae

303. [1]*Collinsonia canadensis* L.
304. *Lycopus americanus* Muhl.
305. *L. virginicus* L.
306. [2]*Nepeta cataria* L.
307. *Prunella vulgaris* L.
308. *Pycnanthemum muticum* (Michx.) Pers.
309. [4]*P. tenuifolium* Schrad.
310. [4]*Satureja vulgaris* (L.) Fritsch var. *neogaea* Fern.
311. *Scutellaria epilobifolia* A. Hamilton
312. *S. lateriflora* L.
313. [1]*Stachys hyssopifolia* Michx.
314. *Teucrium canadense* L.

Solanaceae

315 [2]*Datura stramonium* L. var. *tatula* (L.) Torr.
316. *Solanum carolinense* L.
317. [2]*S. nigrum* L.

Scrophulariaceae

318. *Gerardia maritima* Raf.
319. *Gratiola aurea* Muhl.
320. *Linaria canadensis* (L.) Dumont
321. [2]*L. vulgaris* Hill.
322. *Lindernia anagallidea* (Michx.) Pennell
323. [2]*Paulownia tomentosa* (Thunb.) Steud.
324. *Scrophularia lanceolata* Pursh
325. [2]*Verbascum thapsus* L.
326. [2]*Veronica serpyllifolia* L.
327. *V. tenella* All.

Bignoniaceae

328. [2]*Catalpa bignonioides* Walt.

Orobanchaceae

329. *Epifagus virginiana* (L.) Bart.

Phrymaceae

330. [1]*Phryma leptostachya* L.

Plantaginaceae

331. *Plantago aristata* Michx.
332. [2]*P. lanceolata* L.
333. *P. major* L. var. *scopulorum* Fries & Broberg
334. *P. oliganthos* R. & S.

Rubiaceae

335. *Cephalanthus occidentalis* L.
336. *Galium aparine* L.
337. *G. palustre* L.
338. *G. tinctorium* L.
339. *G. triflorum* Michx.

Caprifoliaceae

340. [2]*Lonicera japonica* Thunb.
341. *Sambucus canadensis* L.
342. *Viburnum recognitum* Fern.

Campanulaceae

343. *Lobelia inflata* L.

Compositae

344. [2]*Achillea millefolium* L.
345. *Ambrosia artemisiifolia* L.
346. *Anaphalis margaritacea* (L.) C. B. Clarke var. *intercedens* Hara
347. *Antennaria neglecta* Greene
348. [2]*Anthemus cotula* L.
349. [2]*Artemisia stelleriana* Bess.

Compositae (continued)

350. *Aster divaricatus* L.
351. *A. dumosus* L.
352. [1]*A. novae-angliae* L.
353. [4]*A. vimineus* Lam.
354. *Baccharis halimifolia* L.
355. *Bidens cernua* L.
356. *B. connata* Muhl. var. *petiolata* (Nutt.) Farw.
357. *B. frondosa* L.
358. [2]*Chrysanthemum leucanthemum* L. var. *pinnatifidum* Lecoq & Lamotte
359. *Chrysopsis falcata* (Pursh) Ell.
360. [2]*Cichorum intybus* L.
361. *Cirsium altissimum* (L.) Spreng.
362. [2]*C. arvense* (L.) Scop.
363. *C. discolor* (Muhl.) Spreng.
364. *C. horridulum* Michx.
365. [1]*C. muticum* Michx.
366. *C. pumilum* (Nutt.) Spreng.
367. [2]*C. vulgare* (Savi) Tenore
368. *Erechtites hieracifolia* (L.) Raf.
369. *Erigeron pusillus* Nutt.
370. *E. strigosus* Muhl.
371. *Eupatorium hyssopifolium* L.
372. *Gnaphalium obtusifolium* L.
373. *G. uliginosum* L.
374. *Helenium flexuosum* Raf.
375. *Hieracium gronovii* L.
376. [2]*H. praealtum* Gochnat var. *decipiens* W. D. J. Koch
377. [2]*Hypochoeris radicata* L.
378. *Iva frutescens* L. var. *oraria* (Bartlett) Fern.
379. [2]*Lactuca scariola* L. f. *integrifolia* (Bogenh.) G. Beck
380. [2]*Matricaria matricarioides* (Less.) Porter
381. [4]*Mikania scandens* (L.) Willd.
382. [2,4]*Onopordum acanthium* L.
383. *Pluchea purpurascens* (Sw.) DC. var. *succulenta* Fern.
384. *Prenanthes trifoliolata* (Cass.) Fern.
385. *Rudbeckia hirta* L.
386. *Solidago nemoralis* Ait.
387. *S. rugosa* Ait.
388. *S. sempervirens* L.
389. *S. tenuifolia* Pursh
390. [2]*Sonchus asper* (L.) Hill
391. [2]*Taraxacum officinale* Weber
392. *Xanthium echinatum* Murr.
393. [1,2]*X. spinosum* L.

A CONTRIBUTION TOWARDS A VASCULAR FLORA OF THE GREAT DISMAL SWAMP

LYTTON J. MUSSELMAN, DANIEL L. NICKRENT,[1] AND GERALD F. LEVY

This flora is an enumeration of the vascular plants growing without cultivation in the Great Dismal Swamp. It is hoped that this work will be of value to the rapidly increasing number of persons visiting the swamp, particularly since the establishment of the Dismal Swamp National Wildlife Refuge in 1973. Great pains have been taken to ensure completeness of the inventory presented here. Yet, the Dismal Swamp is difficult to botanize, and additional species will undoubtedly be added to the present list. Previous botanical work in the swamp is listed in Kirk *et al.* (in press).

LOCATION AND EXTENT OF AREA

The Great Dismal Swamp, which occupies about 104,000 ha. of North Carolina and Virginia (Figure 1), is one of the largest remaining swamp forests on the Coastal Plain. Although the swamp is considered to be centered around Lake Drummond in the Virginia cities of Suffolk and Chesapeake, it extends into the North Carolina counties of Currituck, Camden, Perquimans, Gates, and Pasquotank. Except for the western edge, which is delimited by the Suffolk Escarpment (Henry, 1970), the boundaries of the swamp are not sharply defined.

TOPOGRAPHY AND DRAINAGE

The Dismal Swamp is situated on a low, poorly drained flat marine terrace which ranges from 4.5 to 7 m. above sea level (Wingo, 1949). Drainage in the swamp is largely controlled by an extensive system of ditches constructed over the last two hundred years. Four major ditches were constructed in the eighteenth and nineteenth centuries. The oldest (Washington Ditch) flows into Lake Drummond from the west. Feeder Ditch flows out of

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[1]National Science Foundation Undergraduate Research Participant, summer 1975.

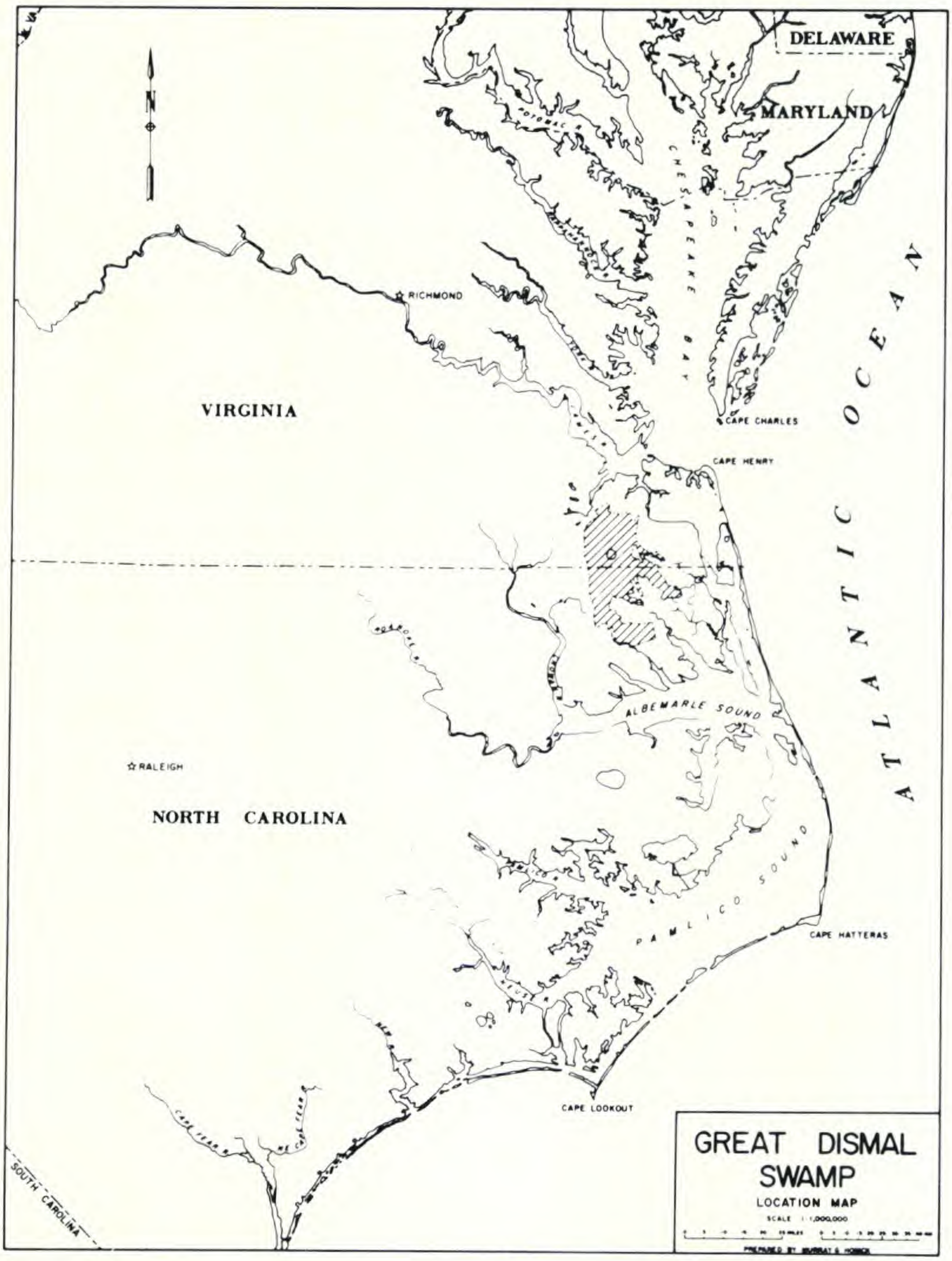


Figure 1. General location of the Great Dismal Swamp in Virginia-North Carolina.

Lake Drummond into Dismal Swamp Canal and thence into Albemarle Sound via the Pasquotank River. Riddick Ditch flows into the lake from the south, and Jericho Ditch enters the lake from the northwest (Reid, 1952). With the exception of Portsmouth Ditch (dug in the early 1800's) most other ditches were constructed during the twentieth century. Drainage is partially regulated by a system of control gates. The Northwest River (draining to the southeast) and the Pasquotank River probably were the major outflows of the original drainage.

SOILS

Most of the soils of the swamp are highly organic and very acidic. Inorganic soils include sand, silt, and clay deposited as low terraces and fluvial silts, and clays extending from the Suffolk Escarpment (Henry, 1970).

The most extensive soil type is mucky peat which ranges in depth from 1 to 4.5 m. and occupies about 75% of the total swamp area. This soil is intermediate between peat in which vegetable materials are recognizable and muck in which they are not. The deepest deposits lie to the north of Lake Drummond. In many areas peat depth has been reduced by fire (Henry, 1970). Shallow mucky peat over loam and over sand are other soil types. Mucky peat gradually intergrades with poorly drained inorganic soils at some places.

The history of the development of the peat and other underlying substrates has been discussed in detail by Whitehead (1972) who postulated that the underlying sediment was dissected by meandering, slow-flowing streams. Peat deposition seems to have begun in these streams and eventually to have overtopped the interfluvial areas perhaps in the manner of a blanket bog.

CLIMATE

The region is characterized by mild winters and long humid summers. Mean temperatures, based on an 85 year record for Norfolk County, are: winter, 6.5°C.; spring, 17.3°C.; summer, 25.3°C.; and fall, 17.3°C. The average growing season is 237 days, and the average annual precipitation for Wallaceton on the swamp's eastern edge is 131.25 cm. Rainfall is most abundant during the growing season.

VEGETATIONAL HISTORY

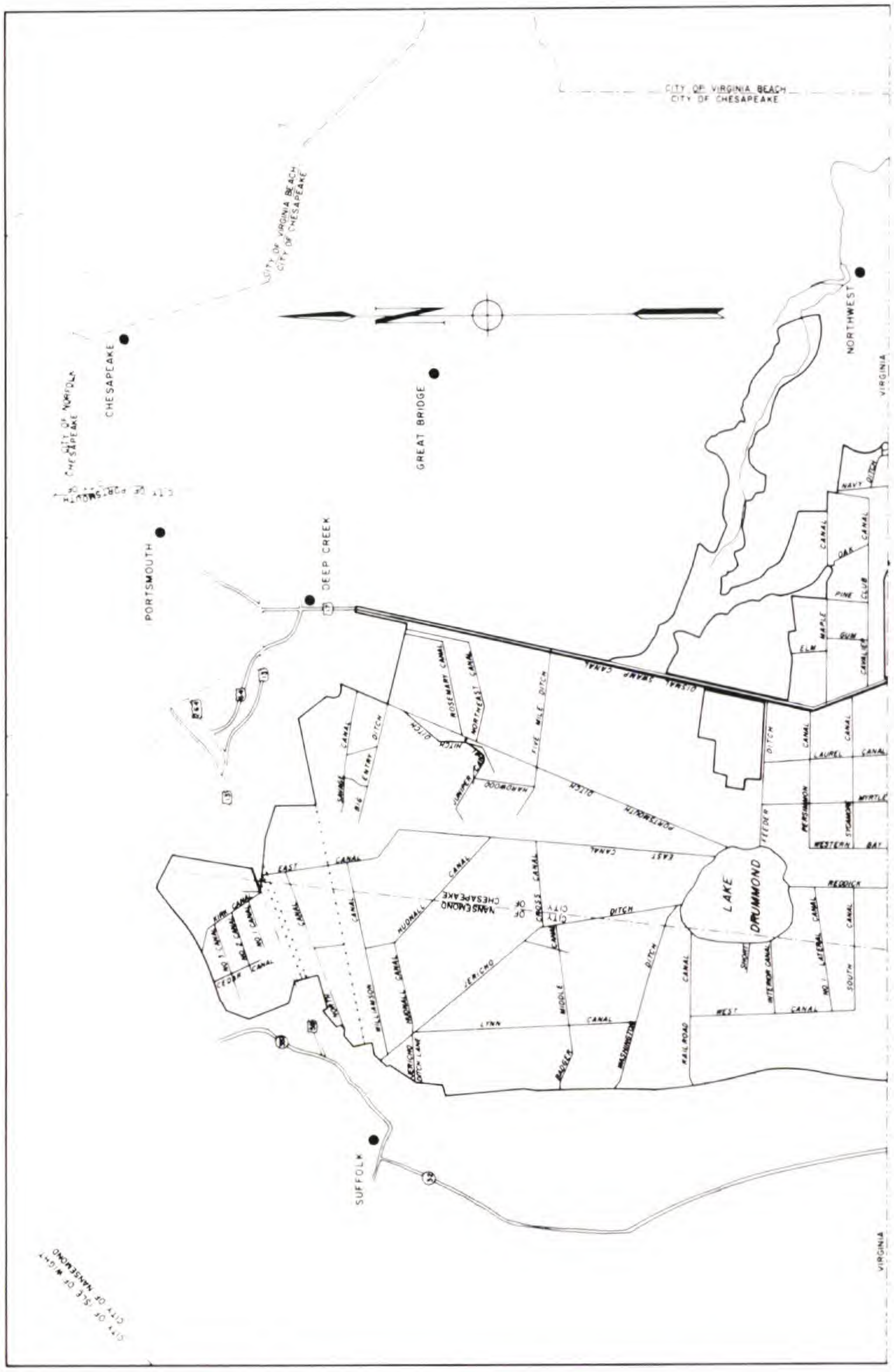
The vegetational history of the Dismal Swamp as revealed by palynological studies (Cocke, 1928; Whitehead, 1972) can be summarized as follows: 1) 14,000–10,000 B.P. — exposure of Dismal Swamp terrace, cutting by meandering streams, and colonization by marsh communities with boreal forest on the interfluvials; 2) 10,000–8,000 B.P. — peat accumulation continues, interfluvial vegetation a northern hardwoods-mixed forest association; 3) 8,000–4,000 B.P. — oak hickory forest association and lowland forest species; and 4) 4,000–300 B.P. — gum-cypress forest. Though greatly simplified, these major trends correspond to the gradual climatic warming which has occurred during the last 14,000 years.

Kearney (1901) appears to be the first to execute an extensive study of the Dismal Swamp. Col. William Byrd's descriptions (in Kearney, 1901) suggest that extensive stands of cypress (*Taxodium distichum*) interspersed by blow-downs and various stages of secondary succession occurred in the 1700's. The first timber to be removed seems to have been cypress which often became replaced by single-aged stands of Atlantic white cedar (*Chamaecyparis thyoides*) also known as "juniper" (Kearney, 1901). Subsequently cedar was extensively cut (Brown, 1970).

Kearney (1901) described two hygric forest communities. "Dark Swamp" included *Nyssa sylvatica, Taxodium distichum,* and *Acer rubrum.* Also mentioned were *Pinus taeda,* which was especially important on higher ground near the border of the swamp, and *Fraxinus caroliniana* and *Quercus phellos.* Important smaller trees listed by Kearney were *Magnolia virginiana, Persea borbonia, Carpinus caroliniana, Salix nigra, Alnus rugosa,* and *Populus heterophylla. Liriodendron tulipifera* and *Liquidambar styraciflua* were associated with *Pinus taeda* at the edge of the swamp.

"Light Swamp" was divided into the following four associations: 1) "juniper," i.e. *Chamaecyparis* forest; 2) Ericaceae; 3) *Arundinaria gigantea;* and 4) *Woodwardia* (*Anchistea*) — *Sphagnum.*

"Juniper" forest association occurred most often at the periphery of the swamp (Kearney, 1901) with *Chamaecyparis thyoides* dominant. By 1899 much of the extensive "juniper" forest had been commercially cut, and although some dense "juniper" forest stands remained, most were scattered through a matrix of other species. Where "juniper" was cut, populations of *Pinus taeda, Magnolia virginiana, Persea borbonia, Ilex opaca, Acer rubrum,* and *Nyssa*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NORTHWEST
VIRGINIA
PORTSMOUTH
DEEP CREEK
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LAKE DRUMMOND
NANSEMOND
CITY OF NANSEMOND
CITY OF SUFFOLK
CANAL
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RAILROAD

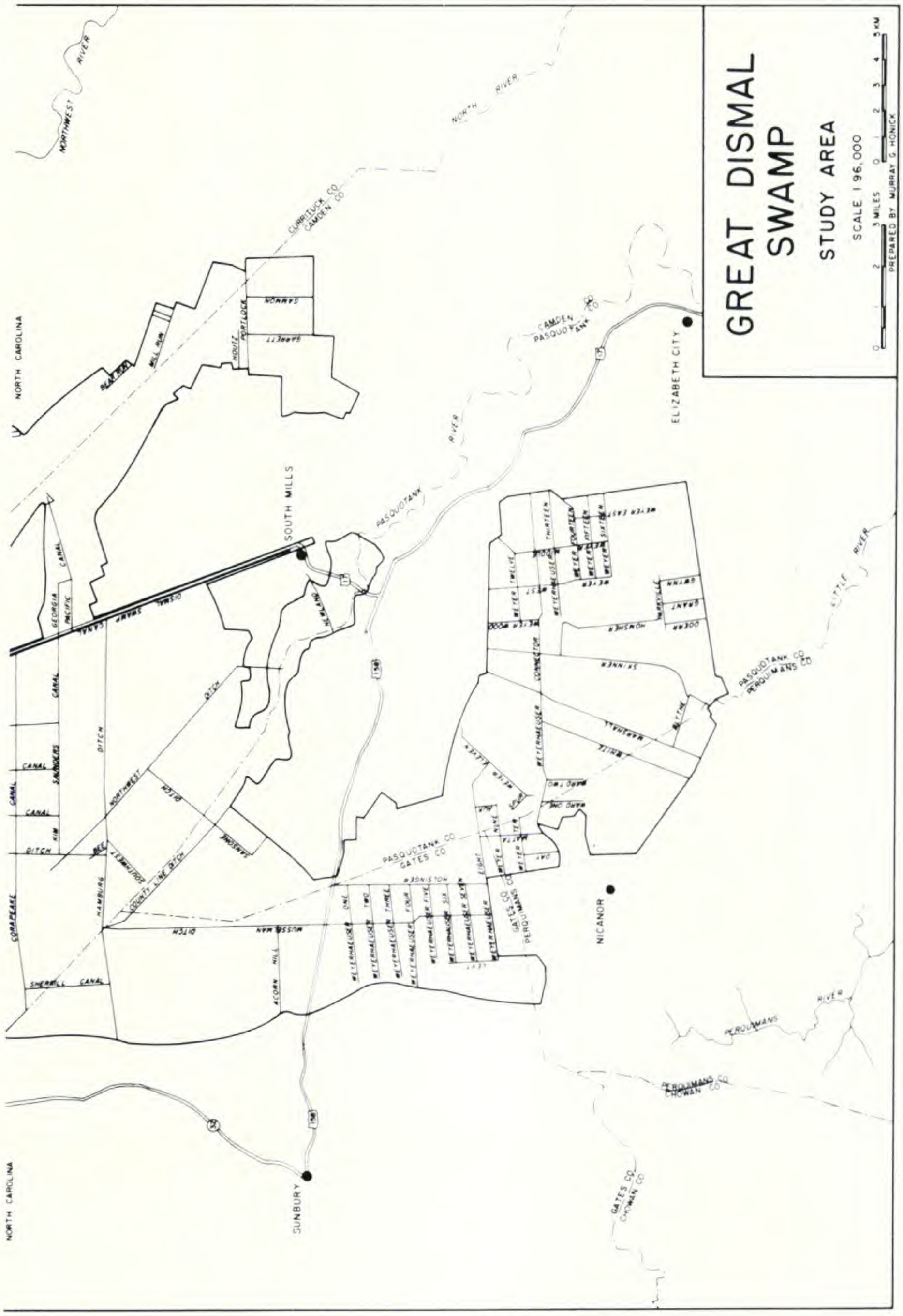

Figure 2. Great Dismal Swamp study area.

sylvatica expanded. On better drained soils *Quercus nigra, Q. michauxii,* and *Fagus grandifolia* replaced "juniper" forest.

The shrub association occurred in clear-cut areas and in areas with scattered regeneration. The most important species cited by Kearney (1901) were: *Clethra alnifolia, Itea virginica, Lyonia ligustrina, L. lucida, Leucothoë racemosa, Ilex glabra, Azalea viscosa,* and *Vaccinium corymbosum.* This association was described by Kearney (1901) as ". . . rapidly increasing in the interior of the Dismal Swamp, where it is said to have been once almost unknown." Today extensive areas of a holly-pond pine community occur in extreme southern portions of Virginia and northern North Carolina. The dominants appear to differ from those described by Kearney since *Ilex glabra* rather than *Clethra alnifolia* contributes most to this association's physiognomy.

The *Arundinaria* association was described as covering extensive areas in nearly pure stands. This association is at present of isolated occurrence.

Kearney's *Woodwardia — Sphagnum* association is not obvious at the present time.

PRESENT VEGETATION

Until 1937 approximately 8,000 ha. of virgin timber remained in the southwest portion of the swamp in Virginia; now practically none exists. Recent studies on the vegetation of the Great Dismal Swamp (Levy & Walker, in press) have shown that its composition has been greatly altered in the past 75 years. Comparison of the current composition of the understory and overstory with historical descriptions documents a strong successional trend to more mesic, less swamp-like conditions.

The present vegetation of the Dismal Swamp is composed of several community types. Almost pure stands of *Acer rubrum* and *Nyssa sylvatica* occur on peat throughout the swamp. A few individuals of *Chamaecyparis thyoides* are found in this association, which suggests that certain areas were once selectively cut for "juniper." Those sites with less peat and some mineral soil support a mixed deciduous forest, which shows less evidence of recent disturbance. *Acer rubrum* and *Nyssa sylvatica* are common species but are particularly abundant on thicker peat deposits. Species of *Fraxinus* are often co-dominant in wetter areas and *Liquidambar styraciflua* and *Pinus taeda* are co-dominants in relatively drier areas.

Future trends in the vegetation, as indicated by sapling composition, suggest a continuum with *Fraxinus* species becoming more important in wetter areas. *Ilex opaca, Nyssa sylvatica,* and *Persea borbonia* are increasing in areas having fluctuation between wet and dry extremes. *Acer rubrum* appears to be increasing in importance through the swamp in both wetter and drier situations. Stands currently dominated by *Chamaecyparis thyoides* may eventually be eliminated from the swamp due to the lack of fire.

Included among the collection sites are a number of disturbed areas with weeds. These areas include a borrow pit, an abandoned home site, ditch banks, cut over forest stands and burns.

"Mesic islands" represent areas of relatively high ground surrounded by swamp. In general these areas tend to be near the western edge of the swamp. Among the canopy species are *Fagus grandifolia, Quercus nigra, Q. phellos, Q. laurifolia, Q. velutina* and *Q. michauxii.* Often present are *Ostrya virginiana, Carpinus caroliniana, Ulmus americana, Liriodendron tulipifera* and *Fraxinus americana.* The ubiquitous *Acer rubrum* is also important. The North Carolina islands are especially noticeable on high level infrared aerial photographs. Among the unusual species found in these mesic areas are *Stewartia malacodendron* and *Trillium pusillum.*

Ditches and ponds are characterized by tannin-stained, dark, low pH (2–5.8) "juniper" water. Characteristic plants are species of *Utricularia, Callitriche heterophylla, Ludwigia palustris, Proserpinaca palustris,* and *Juncus repens.*

METHODS AND MATERIALS

Our data is based on field work conducted from July, 1973, to August, 1976. Collection data on some species was obtained from herbarium specimens at the U. S. National Herbarium (US). Collections are deposited in the herbarium of Old Dominion University (ODU) with duplicates of most specimens at NCU and VPI. The arrangements of families and nomenclature generally follow Radford *et al.* (1968). No attempt has been made to distinguish species which may have been introduced.

In order to provide accurate locality data, we have listed representative collection sites. The collection site of each species may be determined by the letter-number code which follows the species name.

KEY TO COLLECTION SITES

1. City of Suffolk (Nansemond), Virginia
   - A. Five year old sweet gum-red maple stand just south of Seaboard Coastline Railroad, 0.5 mi. W. of Chesapeake city limits.
   - B. Borrow pit, Jericho Ditch Lane at escarpment.
   - C. Beech-maple stand and surrounding low areas on Jericho Ditch, 0.5 mi. S. of Williamson Ditch.
   - D. Abandoned cabin site at junction of Jericho Ditch and Jericho Ditch Lane.
   - E. Gum forest, northeast of the junction of Lynn and Washington Ditches.
   - F. Banks and waters of Washington Ditch.
   - G. Lake Drummond at Washington Ditch.
   - H. Banks and waters of West Ditch.
   - I. Mature gum-poplar forest along west edge of Lake Drummond just south of West Ditch.
   - J. Roadsides and shallow water near road 604, 6.4 mi. N. of state line.
   - K. Beech-pine forest east of road 604, 2.4 mi. N. of state line.
   - L. Cutover forest, 2 mi. W. of Old Norfolk Road, southeast of Driver.
   - M. Power line right-of-way west of Jericho Ditch.

2. City of Chesapeake, Virginia
   - A. Banks and waters of Dismal Swamp Canal, 1 mi. N. of state line.
   - B. Open, burned area 1 mi. W. of U.S. 17, 1 mi. S. of Feeder Ditch.
   - C. Mature gum-poplar forest on east edge of Lake Drummond south of Portsmouth Ditch.
   - D. Waters of eastern portion of Lake Drummond between East Ditch and Lake Ditch.
   - E. Cypress-tupelo forest along Portsmouth Ditch just south of Big Entry Ditch.

3. Gates County, North Carolina
   - A. Marsh north of Hamburg Ditch, 1 mi. E. of road 1332.
   - B. "Mesic island" north of Hamburg Ditch, 1.5 mi. E. of road 1332.
   - C. Cypress-tupelo forest, south of Hamburg Ditch, just E. of escarpment.
   - D. "Mesic island," 1.5 mi. N. of highway 158, just E. of Pasquotank County line.
   - E. Cypress-tupelo forest just S. of U.S. 158, 1 mi. E. of road 1002.
   - F. Ditch and surrounding burned area north of U.S. 158, just E. of county line.

4. Camden County, North Carolina
   - A. Cutover Atlantic white cedar stand, west of Western Boundary Ditch, just south of state line.
   - B. Cypress-tupelo swamp at end of road 1219, four miles northwest of South Mills.
   - C. Shallow water and margins of small stream at U.S. 17 bridge, 1.7 mi. S. of South Mills.
   - D. Undeveloped state park just south of state line and west of U.S. 17.

5. Pasquotank County, North Carolina
   - A. Shallow water and margins of Pasquotank River at the end of road 1361.
   - B. Pine-maple forest at end of road 1360.

CATALOG OF SPECIES

LYCOPODIACEAE

Lycopodium obscurum L. Rare. Small population. 1A.
L. complanatum Fern. Rare. Small population. 1A.

SELAGINELLACEAE

Selaginella apoda (L.) Spring. Damp roadside. 1K.

OPHIOGLOSSACEAE

Botrychium dissectum Spreng. Infrequent. Drier sites. North of Washington Ditch at west edge of refuge. Also 3D.

OSMUNDACEAE

Osmunda cinnamomea L. Common in moist soil. 1A, 1C, 1E, 1I, 1K, 2B, 3C, and 4B.
O. regalis var. *spectabilis* (Willd.) Gray. Common in moist soil. 1A, 1E, 1G, 1H, 1I, 1J, 2A, 2D, 3A, 3C, 4B, 4C, and 5A.

PTERIDACEAE

Pteridium aquilinum (L.) Kuhn. Infrequent along roadsides of Jericho, Interior, and Middle Ditches.

ASPIDIACEAE

Athyrium asplenioides (Michx.) Eat. Infrequent. Roadside Jericho Ditch. 3B.
Dennstaedtia punctilobula (Michx.) Moore. Rare. Roadside of Middle Ditch.
Dryopteris celsa (Palmer) Small. Infrequent. Cypress-gum forests. 2C, 3C, 3D, and 4B.
D. cristata (L.) Gray. Rare. 3C and 4B.
D. intermedia (Willd.) Gray. Infrequent. Gum forest. 2C, 3C, and 3D.
D. marginalis (L.) Gray. "Nansemond County." *Palmer 256* (US).
D. spinulosa (Muell.) Watt. Frequent. 1E, 1I, 2C, 3C, and 4B.
Polystichum acrostichoides (Michx.) Schott. Rare. Beech forest. 3B.
Thelypteris noveboracensis (L.) Nieuw. Rare. Roadside of Jericho Ditch.
T. palustris Schott. Rare. Marsh. 3A.

BLECHNACEAE

Anchistea virginica (L.) Presl. Common and abundant. Along roads. Also 1E, 1F, 1H, 1I, 1J, 2A, 2E, 3A, 3C, 4B, 4C, and 5A.

Lorinseria areolata (L.) Presl. Common and abundant. 1E, 1F, 1H, 1I, 1J, 2C, 3A, 3C, and 5A.

ASPLENIACEAE

Asplenium platyneuron (L.) Oakes. Frequent in a variety of habitats. 1A, 1E, 1I, 1K, 1C, 3B, and 4B.

POLYPODIACEAE

Polypodium polypodioides (L.) Watt. Infrequent on tree trunks. Hamburg Ditch. 1C and 5A.

AZOLLACEAE

Azolla caroliniana Willd. Rare. Margins of stream. 4C.

GYMNOSPERMS

PINACEAE

Pinus serotina Michx. Frequent but scattered. Roadsides. 2B and 4A.

P. taeda L. Common on drier sites. Roadsides. Jericho, Lynn, and Washington Ditches. Also 1A, 1K, 3B, 3D, 3E, and 5B.

TAXODIACEAE

Taxodium distichum (L.) Rich. Common. 1C, 1E, 1F, 1G, 1H, 1I, 1J, 2D, 2E, 3C, 3E, 4B, 4C, 5A, and throughout the swamp.

CUPRESSACEAE

Chamaecyparis thyoides (L.) BSP. Common but scattered. Southeast of fire tower, 4A. Several sizable stands south of Lake Drummond.

ANGIOSPERMS

MONOCOTS

TYPHACEAE

Typha latifolia L. Rare. 1B and 3A.

SPARGANIACEAE

Sparganium americanum Nutt. In flowing water of most ditches.

POTAMOGETONACEAE

Potamogeton diversifolius Raf. Rare. Shallow, flowing water of Hamburg Ditch.

P. pulcher Tuckerm. Rare. Standing water. 1J and 3A.

POACEAE

Arundinaria gigantea (Walt.) Muhl. Common and abundant especially in burned areas. 1A, 1C, 1E, 1F, 1G, 1H, 1I, 1K, 1L, 2A, 2B, 2E, 3A, 3C, 4B, and 5B.

Agrostis stolonifera L. Rare. Weedy area. 1D.

Alopecurus carolinianus Walt. Rare. Roadside. 1D.

Andropogon virginicus L. Infrequent. Open weedy areas. 1L, 1M, 2B, and 4A.

Briza minor L. Rare. Roadside. 1D.

Bromus catharticus Vahl. Infrequent. Norfolk and Western Railroad right-of-way. 1D.

B. commutatus Schrader. Rare. 1M.

B. japonicus Thunb. Infrequent. Norfolk and Western Railroad right-of-way. 1D.

B. secalinus L. Rare. 3F.

Calamagrostis cinnoides (Muhl.) Bart. Rare. Roadside, 1J. Marsh, 3A.

Dactylis glomerata L. Rare. Open, disturbed area. 1D.

Echinochloa crusgalli (L.) Beauv. Rare. 1M.

E. walteri (Pursh) Heller. Rare. 1M.

Elymus virginicus L. Rare. 1M.

Eragrostis hirsuta (Michx.) Nees. Rare. Open, disturbed area. 1D.

Erianthus giganteus (Walt.) Muhl. Infrequent. Scattered along roads throughout the swamp. Also Norfolk and Western Railroad right-of-way. 1M.

Festuca myuros L. Rare. Weedy field. 1D.

F. octoflora Walt. Rare. Weedy field. 1D.

Glyceria striata (Lam.) Hitch. Rare. Swamp forest. 1E.

Holcus lanatus L. Rare. 1E.

Hordeum pusillum Nutt. Rare. Weed in field. 1D.

Leersia oryzoides (L.) Swartz. Infrequent. Roadside. 1J and 3F.

L. virginica Willd. Infrequent. Roadside. 1J, swamp forest, 1E.

Lolium multiflorum Lam. Infrequent. Jericho Ditch at Williamson Ditch. Roadsides of Interior Ditch and Hamburg Ditch.

Microstegium vimineum (Trin.) Cam. Rare. Field near fire tower.
Panicum anceps Michx. Infrequent. Cutover and burned areas. 1M and 3F.
P. clandestinum L. Rare. 3F.
P. dichotomum L. Beech forest. 3D.
P. dichotomiflorum Michx. Infrequent. Norfolk and Western Railroad right-of-way. Also 1M.
P. hians Ell. Rare. Old road. 1L.
P. scoparium Lam. Common. Essentially all roadsides.
P. verrucosum Muhl. Abundant in burned area along U.S. 158 but not collected elsewhere.
P. virgatum L. Rare. Burned area. 3F.
Paspalum dilatatum Poir. Rare. Grassy field near fire tower.
P. dissectum L. Rare. Roadside. 1J.
P. laeve Michx. Rare. Power line cut. 1M.
Phragmites communis Trin. Rare. One small stand along Corapeake Ditch.
Poa autumnalis Muhl. ex Ell. Rare. Woods. 1C.
Setaria glauca (L.) Beauv. Rare. 1M.
S. magna Grisebach. Rare. 3F.
Sphenopholis obtusata (Michx.) Scrib. Rare. Marsh. 3A.
Sporobolus poiretii (R. & S) Hitch. Rare. Roadside. 1D.
Uniola laxa (L.) BSP. Rare. Sandy soil. 1C and 3B.

CYPERACEAE

Carex abscondita Mackenzie. Rare. 3C.
C. alata T & G. Frequent. Roadsides. Ditch banks. 1F, 1H, 1J, 1M, 2B, 3F, and 4A.
C. blanda Dew. Rare. Beech forests. 1C and 3B.
C. debilis Michx. Rare. Gum-cypress forest. 3E.
C. emmonsii Dew. Rare. Roadside. 1J.
C. folliculata L. Rare. Ditch bank at junction of Lynn and Badger Ditches.
C. gigantea Rudge. Frequent. Gum-cypress forests. 1E, 1J, 2E, 3C, 3E, and 4B.
C. joori Bailey. Rare. Roadside. 1J.
C. lurida Wahlenb. Common. Borders of intermittent pools and other wet areas. 1C, 1E, 1J, 1M, 3C, 3E, and 3F.
C. swanii (Fern.) Mackenz. Rare. Roadside. Middle Ditch north of Lynn Ditch.

Cyperus erythrorhizos Muhl. Rare. 1M.
C. rivularis Kunth. Rare. Margin of stream. 4C.
C. strigosus L. Rare. 1M.
Dulichium arundinaceum (L.) Britt. Infrequent. Low roadside. Jericho Ditch at Lynn Ditch. Shallow water of Lynn Ditch. 3A and 1 M.
Eleocharis baldwinii (Torr.) Chapm. Rare. Margins of flowing water. 3F.
E. microcarpa Torr. Rare. Margin of ditch. 3F.
E. obtusa (Willd.) Schultes. Rare. 1M.
E. tenuis (Willd.) Schultes. Rare. Shallow water of Hamburg Ditch near 3A.
E. tuberculosa (Michx.) R & S. Margins of small pools. 1M and 3F.
Eriophorum virginicum L. Abundant in sphagnous bog. 4 mi. w. of East Ditch on North Ditch.
Fuirena squarrosa Michx. Rare. Margins of ditch. 4C and 3F.
Rhynchospora corniculata (L.) Gray. Infrequent. Wet roadside. 1J and 1F.
Scirpus cyperinus (L.) Kunth. Common and abundant in open ditches and along roadsides. 1B, 1F, 1H, 1J, 1M, 2B, 3A, 3F, 4C, and 5A.

ARACEAE

Arisaema triphyllum (L.) Schott. Infrequent. 1E. and 3C.
Orontium aquaticum L. Rare. Swamp forest and margin of marsh. 3A.
Peltandra virginica (L.) Schott & Endl. Rare. Margin of marsh. 3A.

LEMNACEAE

Lemna valdiviana Phil. Infrequent. Quiet water. 1F and 4C. Borrow pit on Jericho Ditch Lane.
Spirodela oligorrhiza (L.) Schleid. Infrequent. Floating on quiet water. 1F and 4C. Portions of Jericho and Hamburg Ditches.
Wolffia columbiana Karst. Infrequent. Quiet water, 4C. Also borrow pit on Jericho Ditch Lane.
Wolffiella floridana (J. D. Sm.) C. H. Thompson. Infrequent. Floating just beneath surface of quiet water, 4C. Borrow pit on Jericho Ditch Lane.

XYRIDACEAE

Xyris ambigua Beyrich. Rare. Open, sunny roadside. Corapeake Ditch.

BROMELIACEAE

Tillandsia usneoides L. Infrequent. On trees in Lake Drummond, 2D; 5A.

COMMELINACEAE

Commelina virginica L. Infrequent. Roadsides and ditches. Banks in full sun. 1F, 1H, 1J, and 2A.

PONTEDERIACEAE

Pontederia cordata L. Rare. Shallow ditch at margin of marsh. 3A.

JUNCACEAE

Juncus bufonis L. Rare. Margin of small stream. 4C.

J. effusus L. Common. Essentially any open wet area. 1B, 1F, 1G, 1H, 1J, 3A, 3C, 3F, 4B, and 5A.

J. repens Michx. Infrequent. Shallow water and shores, 1J and 4C. Shores of Lake Drummond where it is the only submergent vascular plant.

J. tenuis Willd. Infrequent. Roadsides. 1J and 1M.

Luzula multiflora (Retz.) Lejeune. Infrequent. Beech forests. 1C, 1K, and 3D.

LILIACEAE

Smilax rotundifolia L. Ubiquitous; in essentially any open area.

S. glauca Walt. Ubiquitous; in essentially any open area.

S. laurifolia L. Ubiquitous; in essentially any open area.

S. walteri Pursh. Rare. Open roadsides. 4C.

Trillium pusillum Michx. Rare. Beech forest. 1C.

Hemerocallis fulva L. Rare. Roadside. Washington Ditch.

Medeola virginiana L. Infrequent. Beech forests. 1C, 1K, and 3B.

IRIDACEAE

Sisyrinchium angustifolium Miller. Infrequent. Roadsides. Jericho Ditch and Interior Ditch.

Iris virginica L. Rare. Marsh. 3A.

ORCHIDACEAE

Cypripedium acaule Ait. Rare. Beech forest. 1K.

Listera australis Lindl. Infrequent. Swamp forest, 2E. Beech forest, 1K.

Goodyera pubescens (Willd.) R. Brown. Infrequent. Beech forests. 1C, 1K, and 3B.

Tipularia discolor (Pursh) Nutt. Infrequent. Beech forest. 1C and 3B.

Habenaria clavellata (Michx.) Spr. "Great Dismal Swamp," *Kearney 1648* (US).

DICOTS

SAURURACEAE

Saururus cernuus L. Common. In standing water. 1F, 1G, 1H, 1J, 2A, 2D, 3F, 4C, 4B, and 5A.

SALICACEAE

Salix nigra Marsh. Infrequent. Stream and ditch margins. 1F, 2A, and 3F.

Populus deltoides Marsh. Single tree along Laurel Ditch at state line.

P. heterophylla L. Common. Swamp forests. 1E, 1I, 1J, 1L, 2E, 3C, 3E, 4C, and 5A.

MYRICACEAE

Myrica cerifera L. Common. Roadsides along Corapeake Ditch.

BETULACEAE

Alnus serrulata (Ait.) Willd. Frequent. Ditch banks and margins of small streams. 1G, 1H, 2D, 3F, 1J, and 4C.

Betula nigra L. Rare. Low woods. 2E.

Carpinus caroliniana Walt. Infrequent. Beech stands. 1C, 1K, 3B, and 3D.

Ostrya virginiana (Mill) K. Koch. Infrequent. Beech stands. 1C, 1K, 3B, and 3D.

FAGACEAE

Castanea pumila (L.) Miller. Rare. One tree along Jericho Ditch near Williamson Ditch and one on north side of Hwy 460.

Fagus grandifolia Ehrh. Infrequent. Usually associated with sandy soils. 1C, 1K, 3B, and 3D.

Quercus falcata Michx. var. *pagodaefolia* Ell. Infrequent. 1C, 1K, 1E, 1F, 4D, and 5B.

Q. laurifolia Michx. Frequent. 1I, 2C, 3C, 4B, and 4D.

Q. lyrata Walter. Infrequent. 1J and 1K.

Q. marilandica Muenchh. Single tree along Weyerhaeuser Ditch 4.

Q. michauxii Nutt. Common throughout the swamp. 1A, 1C, 1E, 1I, 2C, 2E, 3C, 3E, 4B, and 5A.
Q. nigra L. Common. Drier areas. 1C, 1E, 1I, 1K, 2A, 2E, 3C, 3E, 4B, and 5A.
Q. velutina Lam. Rare. Roadside. Jericho Ditch.

ULMACEAE

Ulmus americana L. Rare. Roadside. Jericho Ditch.

MORACEAE

Morus rubra L. Rare. Edge of Jericho Ditch Lane.
M. alba L. Rare. Edge of Jericho Ditch Lane.

URTICACEAE

Boehmeria cylindrica (L.) Swartz. Common in open, wet areas. 1E, 1F, 1G, 1H, 1J, 2A, 3A, 3F, 4B, 4C, 4D, and 5A.

LORANTHACEAE

Phoradendron serotinum (Raf.) M. C. Johnston. Common and abundant on a variety of trees (but favoring red maple) throughout the swamp.

POLYGONACEAE

Rumex crispus L. Infrequent. Roadside weed. Railroad Ditch, Interior Ditch, West Ditch, and probably elsewhere.
R. conglomeratus Murray. Abundant along most roads throughout the swamp.
Tovara virginiana (L.) Raf. Common. Low woods. 1E, 2A, 2E, 3C, 3E, 3F, 4B, and 5A.
Polygonum hydropiperoides Michx. Common in wet situations. 1F, 1G, 1H, 1J, 2D, 3F, 4C and 5A.
P. pensylvanicum L. Common in wet situations. 1F, 1G, 1H, 2D, 3F, 4C, and 5A.
P. punctatum L. Rare. Margin of ditch. 3F.
P. sagittatum L. Infrequent. Open damp roadside, 1J; burned area, 3F.

CHENOPODIACEAE

Chenopodium album L. Rare. Right-of-way. 1M.

PHYTOLACCACEAE

Phytolacca americana L. Common but scattered. Essentially any open disturbed area.

CARYOPHYLLACEAE

Stellaria media (L.) Cyrillo. Abundant along damp roadsides throughout the swamp.

CERATOPHYLLACEAE

Ceratophyllum echinatum Gray. Rare. Submergent in shallow water at 4C.

NYMPHAEACEAE

Nuphar luteum (L.) Sibthorp & Smith. Infrequent in shallow ditches along U.S. 158 and at 4D.

RANUNCULACEAE

Clematis viorna L. Rare. Roadside. 1G.

Ranunculus abortivus L. Infrequent. Low woods. 1E, 1J, 1K, and 3F.

BERBERIDACEAE

Podophyllum peltatum L. Rare. Beech stand at 3B.

MAGNOLIACEAE

Liriodendron tulipifera L. Common at drier sites. 1A, 1C, 1E, 1I, 1K, 2C, 3B, 3E, 4B, and 5B.

Magnolia grandiflora L. Rare. Two small trees. Sherrill Ditch and East Ditch.

M. virginiana L. Abundant, especially along roads. 1A, 1C, 1E, 1F, 1H, 1I, 1J, 1K, 1L, 1M, 2B, 2C, 2E, 3C, 3E, 3F, 4A, 4D, and 5B.

ANNONACEAE

Asimina triloba (L.) Dunal. Especially common on peaty soils but found throughout the swamp. 1C, 1E, 1H, 1I, 2C, 3C, 3E, 4B, and 5B.

LAURACEAE

Persea borbonia (L.) Spreng. (incl. *P. palustris).* One of the most abundant shrubs, especially along roads. 1A, 1E, 1I, 1L, 2B, 2C, 3C, 3E, 4A, 4B, and 5B.

Sassafras albidum (Nutt.) Nees. Infrequent. Drier sites. 1A, 1D, 1K, 2B, 3B, and 5B.

BRASSICACEAE

Lepidium virginicum L. Rare. Weedy field. 1D.

Brassica napus L. Rare. Weedy roadside of Jericho Ditch Lane.

Cardamine hirsuta L. Common and abundant along roads throughout the swamp. 1D, 1H, 1J, 1M, 1F, and 4C. Also along Headley Ditch near state line.

SAXIFRAGACEAE

Decumaria barbara L. Common throughout the swamp but seldom flowering except in full sun. 1E, 1I, 2C, 2E, 3C, 3E, 4B, 4D, and 5B.

Itea virginica L. Common in cypress-gum stands. 1C, 1E, 2A, 2D, 2E, 3C, 3E, 4B, 4C, and 5A.

HAMAMELIDACEAE

Hamamelis virginiana L. Rare. Beech stand. 3D.

Liquidambar styraciflua L. Infrequent. Drier sites. 1A, 1C, 1K, 1M, and 5B.

PLATANACEAE

Platanus occidentalis L. Infrequent. Margins of cypress-gum swamps. 1C, 1E, 1I, 2A, 3C, and 5A.

ROSACEAE

Amelanchier canadensis (L.) Med. Common. Roadsides and other habitats. 1C, 1K, 1M, 2B, and 5B.

Aronia arbutifolia (L.) Ell. (*Sorbus arbutifolia* (L.) Heyn.). Rare. 2B.

Crataegus marshallii Eggl. Single tree at junction of Sycamore and Myrtle Ditches.

C. phaenopyrum (L.f.) Med. Infrequent. Drier sites throughout the swamp including 1C, 1K, and 2C.

Duchesnea indica (Andrz.) Focke. Common along roadsides throughout the swamp including 1D, 1F, 1H, 1J, and 4C.

Fragaria virginiana Duchesne. Infrequent. Open sunny areas along Jericho Ditch Lane and field at fire tower.

Potentilla canadensis L. Rare. Roadside, Jericho Ditch Lane.

Prunus angustifolia Marsh. Small population along Jericho Ditch Lane.

P. persica (L.) Batsch. Single small tree. Jericho Ditch Lane.

P. serotina Ehrh. Rare. Roadside. Jericho Ditch Lane.

Rosa palustris Marshall. Common. Open areas, especially banks of ditches.

Rubus argutus Link. Common in disturbed and open areas. 1A, 1L, 2B, 3F, and 4A.

R. cuneifolius Pursh. Common in disturbed and open areas including 1A, 1L, 2B, 3F, 4A, and 5B.
R. hispidus L. Infrequent. Edge of Washington Ditch near west boundary of refuge. 1C, 3B, and 3D.
Spiraea tomentosa L. Rare. Burned area north of Sycamore Ditch just west of Dismal Swamp Canal.

FABACEAE

Cassia fasciculata Michx. Abundant along roads in dry, open situations.
Lespedeza cuneata (Dumont) G. Don. Infrequent along roads. Badger Ditch near Middle Ditch. Railroad Ditch near Western boundary of refuge.
Trifolium pratense L. Rare. Open field near fire tower.
T. repens L. Rare. Camping area near locks of Feeder Ditch.

LINACEAE

Linum virginianum L. Rare. Roadside. Lynn Ditch near Washington Ditch.

OXALIDACEAE

Oxalis dilleni Jacq. Common along all roads in sunny, open habitats.

GERANIACEAE

Geranium carolinianum L. Rare. Open weedy area. 1D.

EUPHORBIACEAE

Acalypha rhomboidea Raf. Infrequent in drier soil in open, sunny areas. 1D, 1L, 2B, and 4A.
Euphorbia maculata L. Infrequent. Roadsides in open areas. Very abundant in areas which have been logged as 4A.

CALLITRICHACEAE

Callitriche heterophylla Pursh. Infrequent submergent of shallow water. 1J and 1F.

ANACARDIACEAE

Rhus copallina L. Common along roads and at 1A, 1D, 1L, 1F, 1H, 2A, and 5B.
R. radicans L. Ubiquitous vine throughout the swamp.
R. vernix L. Infrequent. Roadsides. Corapeake Ditch near recent railhead. West Ditch just south of Interior Ditch. Scott Ditch near North Ditch.

CYRILLACEAE

Cyrilla racemiflora L. Rare. Small population at 2A.

AQUIFOLIACEAE

Ilex coriacea (Pursh) Chapm. Rare. Apparently the northern limit of this species. 1C.

I. decidua Walt. Infrequent. Recent railhead on Corapeake Ditch. Border of field at fire tower. Also 4A.

I. glabra (L.) Gray. Common roadside shrub. Also abundant in recent burns as 2B.

I. opaca Aiton. Common, but best developed in mature forests. 1C, 1I, 2C, 3B, and 3D.

I. verticillata (L.) Gray. Rare. Swamp forest SE of Railroad Ditch.

CELASTRACEAE

Euonymus americanus L. Infrequent. Roadside West Ditch just north of Interior Ditch. Washington Ditch at Lynn Ditch. Also 1C.

ACERACEAE

Acer rubrum L. Ubiquitous. The most abundant tree in the swamp.

BALSAMINACEAE

Impatiens capensis Meerb. Infrequent. Margins of intermittent pools. 1C, 1H, 1J, and 3E.

I. pallida Nutt. Rare. Highway 17 at Wallaceton.

RHAMNACEAE

Berchemia scandens (Hill) K. Koch. Common. 1C, 1E, 1I, 1L, 2C, 2E, 3C, 3E, 4B, and 4D.

VITACEAE

Parthenocissus quinquefolia (L.) Planch. Infrequent in drier areas. 1C, 1K, 1M, and 5B.

Vitis labrusca L. Often with the above species. Abundant throughout the swamp.

V. rotundifolia Michx. Abundant throughout the swamp.

THEACEAE

Stewartia malacodendron L. Infrequent on drier, usually sandy sites. 1C and 3D. Also north of U.S. 460, City of Portsmouth, Virginia.

HYPERICACEAE

Hypericum hypericoides (L.) Crantz. Common on roadbanks throughout the swamp.

H. mutilum L. Common along roads. 1A, 1B, 1D, 1F, 1H, 1J, 1L, 2B, 3F, 4A, and 4C.

H. walteri Gmelin. Rare. Decaying stump in Lake Drummond south of Interior Ditch.

H. virginicum L. Infrequent. Usually found in decaying stumps in water. 1F, 1G, 1J, 2D, and 5A.

VIOLACEAE

Viola papilionacea Pursh. Rare. Roadside. Hamburg Ditch near Sherrill Ditch.

V. primulifolia L. Infrequent. Roadsides. 1J, 1F, and 1K.

PASSIFLORACEAE

Passiflora incarnata L. Infrequent. Roadside along Feeder Ditch 2.0 miles east of Lake Drummond. Banks of Dismal Swamp Canal along U.S. 17 at Feeder Ditch.

LYTHRACEAE

Decodon verticillatus (L.) Ell. Infrequent. Shallow waters of Lake Drummond, 1G and 2D. South of Interior Ditch. Margin of ditch west of canal, 4D.

MELASTOMATACEAE

Rhexia virginica L. Rare. Bank of Dismal Swamp Canal, just south of state line, Camden Co., North Carolina.

R. mariana L. Common. Roadsides, ditch banks, and power lines. 1D, 1F, 1H, 1J, 1M, 2B, 3F, and 4A.

ONAGRACEAE

Ludwigia alternifolia L. Common. Roadsides. 1D, 1J, 2A, 3F, 1L, and 4A.

L. decurrens Walt. Rare. Margin of Lake Drummond south of Feeder Ditch. City of Chesapeake.

L. glandulosa Walt. Rare. 1M.

L. linearis Walt. Rare. Margin of Lake Drummond south of Feeder Ditch. City of Chesapeake.

L. palustris (L.) Ell. Common. Shallow water of all ditches, usually in full sun. 1F, 1H, 1J, 2A, 3A, 3F, 4B, 4C, and 5A.

HALORAGACEAE

Proserpinaca palustris L. Common. Shallow water and margins of ditches and pools. 1B, 1F, 1H, 1J, 1M, 2B, 3A, 3F, 4B, 4C, and 5A.

Myriophyllum heterophyllum Michx. Not seen by authors but several specimens at US.

ARALIACEAE

Aralia spinosa L. Common and abundant. Along all roads.

APIACEAE

Chaerophyllum tainturieri Hook. Infrequent. Roadsides, 1D and 1J. Jericho Ditch near fire tower.

Daucus carota L. Common. Open, sunny area. 1J and 1L. Roadsides throughout the swamp.

Eryngium prostratum Nutt. Rare. Moist ditchbank. 1K.

Foeniculum vulgare Miller. Rare. Road along Feeder Ditch near Highway 17.

Hydrocotyle umbellata L. Infrequent. Low wet areas. 1H, 1J, 1F, and 1C.

Sanicula canadensis L. Rare. 1C.

NYSSACEAE

Nyssa aquatica L. Common. Swamp forests with cypress. 2E, 3C, 3E, 4B, 4C, 4D, and 5A.

N. sylvatica var. *biflora* (Walt.) Sarg. Common throughout the swamp, including Lake Drummond. 2E, 2C, 2F, 2I, 3C, 3F, 4B, 4D, and 5A.

CORNACEAE

Cornus alternifolia L. f. Rare. 3D.

C. florida L. Infrequent. Drier sites. 1A, 1K, 2D, 3B, and 5B.

CLETHRACEAE

Clethra alnifolia L. Common and abundant. This is perhaps the most abundant shrub throughout the swamp.

ERICACEAE

Chimaphila maculata (L.) Pursh. Infrequent. Mesic areas. 1C, 1K, 3B, and 3D.

Gaultheria procumbens L. Rare. Cedar stand, 1.1 mi. s. of Corapeake Ditch.

Kalmia angustifolia L. Rare. Few plants at 2B.

K. latifolia L. Rare. Junction of Scott and North Ditches. Possibly planted at this site but native in region.
Lyonia ligustrina (L.) DC. Infrequent. Ditch margins. 1E and 1F.
L. lucida (Lam.) K. Koch. Infrequent. 1C and 1F. Also spectacular stands along Jericho and Lynn Ditches.
Leucothoë axillaris (Lam.) D. Don. Frequent. Drier sites. 1C, 1K, 3B, 3D, and 5B.
L. racemosa (L.) Gray. Infrequent. Margins of intermittent pools in cypress-tupelo stands. 2E, 3C, and 4B.
Monotropa uniflora L. Infrequent. North of junction of Lynn and Jericho Ditches. 3D and 5B.
Oxydendrum arboreum (L.) DC. Infrequent. Drier sites. 1C, 1K, 1B, and 5B.
Rhododendron atlanticum (Ashe) Rehder. Infrequent. Roadsides. 1C, 2A, and 3F.
R. nudiflorum (L.) Torrey. Infrequent. Widely scattered throughout the swamp. 1C and 1H. Also Lynn Ditch at Jericho Ditch.
Vaccinium stamineum L. Rare. Small population at 1C.
V. corymbosum L. Infrequent. Roadsides. 1J and 1K. Also Jericho Ditch Lane.
V. tenellum Ait. Rare. 1M.

EBENACEAE

Diospyros virginiana L. Infrequent. Drier sites. 1K, 1M, 3B, and 3D.

SYMPLOCACEAE

Symplocos tinctoria (L.) L'Her. Infrequent. Drier sites. 3B and 3D. Scott at North Ditch.

OLEACEAE

Fraxinus caroliniana Mill. Infrequent. Margins of streams. 1J, 1F, and 5A.
F. tomentosa Michx. f. Rare. 1J.
F. pennsylvanica Marsh. Infrequent. Drier sites. 1C, 1I, 2C, and 3D.
Ligustrum sinense Lour. Frequent. Widely scattered along roadsides throughout the swamp.

LOGANIACEAE

Gelsemium sempervirens (L.) Ait. f. This woody vine is ubiquitous throughout the swamp.
Polypremum procumbens L. Rare. Weedy field. 1D.

GENTIANACEAE

Bartonia virginica (L.) BSP. Rare. Old field. 1A.

Gentiana saponaria L. Rare. Edge of Railroad Ditch at refuge boundary.

APOCYNACEAE

Apocynum cannabinum L. Frequent. Roadsides, 1J. Jericho Ditch, Williamson Ditch, and Washington Ditch.

Vinca minor L. Rare. Weedy field. 1D.

VERBENACEAE

Callicarpa americana L. Rare. Roadside. Corapeake Ditch.

Verbena urticifolia L. Rare. Roadsides. Interior Ditch.

LAMIACEAE

Glechoma hederacea L. Infrequent. 1C and roadside, Hamburg Ditch.

Prunella vulgaris L. Common along roadsides.

Salvia lyrata L. Infrequent. Roadsides. 1D and 1J.

Scutellaria integrifolia var. *integrifolia* L. Rare. Roadsides. Railroad Ditch.

Stachys hyssopifolia Michx. Rare. Roadsides. Hamburg Ditch.

Teucrium canadense L. Rare. Roadside. Hamburg Ditch.

SOLANACEAE

Solanum carolinense L. Rare. Dry roadsides. West Ditch.

SCROPHULARIACEAE

Agalinis purpurea (L.) Pennell. Infrequent. Open, sunny areas. 1M and 1J.

Chelone glabra L. Rare. Roadbank. Washington Ditch.

Gratiola neglecta Torr. Rare. Small pool in old logging road 1.0 mile north of U.S. 158, 0.5 mile east of Gates County line.

Paulownia tomentosa (Thunb.) Steud. Infrequent. Small trees. Washington Ditch and Corapeake Ditch.

Verbascum thapsus L. Infrequent. Roadsides. 1C, 1M, and 1J.

Veronica arvensis L. Infrequent. Roadsides, 1C. Also Jericho Ditch Lane.

BIGNONIACEAE

Anisostichus capreolata (L.) Bureau. Ubiquitous throughout the swamp.

Campsis radicans (L.) Seem. Common. Usually in drier areas. 1A, 1C, 1J, 1K, 1L, 1M, 3D, 4D, and 5B.

OROBANCHACEAE

Conopholis virginiana (L.) Wallr. Rare. Beech stand. 3D.

Epifagus virginiana (L.) Bart. Frequent. Always with beech. 1C, 1K, 3B, and 3D. Also beech stands north of U.S. 460 east of Old Norfolk Road.

LENTIBULARIACEAE

Utricularia biflora Lam. Rare. Ditch north of U.S. 158.

U. gibba L. Rare. Shallow waters of Myrtle Ditch.

U. inflata Walt. Rare. Ditch north of U.S. 158.

U. purpurea Walt. Infrequent. Waters of Lynn, Portsmouth, Washington and Interior Ditches.

PLANTAGINACEAE

Plantago aristata Michx. Rare. Hamburg Ditch Road.

P. lanceolata L. Rare. Weedy field. 1D.

P. virginica L. Rare. Weedy area. 1D.

RUBIACEAE

Cephalanthus occidentalis L. Infrequent. Usually in standing water. 1F, 1G, and 1D.

Diodea teres Walt. Rare. Roadsides. Jericho Ditch Lane.

D. virginiana L. Frequent. Usually in roads in full sun. Jericho Ditch Lane, Lynn Ditch, Hudnall Ditch, and North Ditch.

Houstonia caerulea L. Infrequent. Edges of road 604 near 1K and Jericho Ditch north of Hudnall Ditch.

Mitchella repens L. Infrequent. Drier sites. 1C, 3B, and 3D.

CAPRIFOLIACEAE

Lonicera japonica Thunb. Common everywhere except in the very wettest situations.

L. sempervirens L. Rare. Jericho Ditch Lane near 1D.

Sambucus canadensis L. Common. Open, sunny moist areas. 1F, 1H, 1J, 2A, 2B, 3A, 3F, and 4C.

Viburnum nudum L. Rare. Margin of Laurel Ditch south of Sycamore Ditch. Swamp forest 4B.

VALERIANACEAE

Valerianella radiata (L.) Dufr. Infrequent. Weedy roadside, 1J, along U.S. 158.

CAMPANULACEAE

Lobelia cardinalis L. Infrequent. 1J and 3A.

L. nuttallii R. & S. Rare. Wet roadside. 1J.

Specularia perfoliata (L.) A. DC. Rare. Weedy area. 1D.

ASTERACEAE

Achillea millefolium L. Rare. Roadside. Jericho Ditch Lane. 1D.
Ambrosia artemisiifolia L. Rare. Power line cut. 1M.
Aster pilosus Willd. Rare. Power line. 1M.
Baccharis halimifolia L. Infrequent. Roadside, Corapeake Ditch. Power line. 1M.
Bidens frondosa L. Rare. Power line. 1M.
Carduus spinosissimus Walt. Rare. Roadside. Laurel Road south of Persimmon Road.
Crepis japonica (L.) Benth. Infrequent. Roadsides at junction of Jericho and Hudnall Ditches. Also 3F.
Elephantopus tomentosus. Rare. Roadside. Jericho Ditch Lane.
Erechtites hieracifolia (L.) Raf. Parking lot, fire tower.
Erigeron annuus (L.) Pers. Frequent. Roadsides throughout the swamp.
Eupatorium capillifolium (Lam.) Small. Common. This species forms an almost continuous border along drier parts of most roads.
E. coelestinum L. Common. Open roadsides. 1M. Jericho, Corapeake, and Lynn Ditches.
E. hyssopifolium L. Rare. Power line. 1M.
E. maculatum L. Power line. 1M
E. rotundifolium L. Rare. Power line. 1M.
Gnaphalium obtusifolium L. Infrequent. Edge of Williamson Ditch. Also 1D.
Helenium amarum (Raf.) H. Rock. Rare. Power line. 1M.
Hypochoeris radicata L. Rare. Roadside. Jericho Ditch Lane near junction with Jericho Ditch.
Mikania scandens (L.) Willd. Rare. Open roadside. 1J.
Pluchea camphorata (L.) DC. Rare. Open roadside. 1J.
Pyrrhopappus carolinianus (Walt.) DC. Rare. Weedy areas. 1D.
Senecio tomentosus Michx. Infrequent. Roadside. Railroad Ditch near Interior Ditch, open area, 1D.
Solidago erecta Pursh. Rare. Power line. 1M.
Taraxacum officinale Weber. Frequent. Weedy areas, 1D. Field near fire tower, 1M. Also Interior Ditch.

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"A later trip would doubtless reveal many more species, but with the drawback of possible chills and certain yellow flies and mosquitoes."

J. W. Chickering, Jr., 1874

"The flora of the swamp, it must be confessed, is rather tame and monotonous; but if it were possible to penetrate into the remoter fastnesses, many new names would doubtless be added to systematic botany."

B. McCarthy, 1884

"It is very certain that a well-equipped botanical expedition would find much of interest in the unexplored parts of this particular region."

C. L. Pollard, 1896

L. J. M.
DEPARTMENT OF BIOLOGICAL SCIENCES
OLD DOMINION UNIVERSITY
NORFOLK, VIRGINIA 23508

D. L. N.
Present Address
DEPARTMENT OF BOTANY
SOUTHERN ILLINOIS UNIVERSITY
CARBONDALE, ILLINOIS 62901

G. F. L.
DISMAL SWAMP PROGRAMS
OLD DOMINION UNIVERSITY
NORFOLK, VIRGINIA 23508

ULTRAVIOLET LIGHT REFLECTION AND ABSORPTION PATTERNS IN POPULATIONS OF RUDBECKIA (COMPOSITAE)

WARREN G. ABRAHAMSON AND KENNETH D. MCCREA

Coevolution has produced intricate relationships between entomophilous flowers and their insect pollinators. These relationships are established by means of one or more floral attractants (visual phenomena, odor, nectar, pollen, etc.). Visual attraction of pollinators involves not only the shape and size of the flower but also its color(s) and the contrast of the flower with its surroundings. In addition, patterns of contrasting color are present in many flowers (nectar guides) and may take a variety of forms such as concentric circles, lines which radiate from the center, or blotches of color. Daumer (1956, 1958) showed that many nectar guides consist of patterns of differential ultraviolet (UV) reflection which are visible to most pollinating insects.

This study examines intraspecific and interspecific variation in the ultraviolet nectar guide patterns in populations of three species of *Rudbeckia*.

MATERIALS AND METHODS

Seven populations of *Rudbeckia hirta* (sensu most auth., not L.; *R. serotina* Nuttall), five populations of *R. triloba* L., and five populations of *R. laciniata* L. (Fernald, 1950) were sampled during their respective blooming periods in 1974. Initially, all ray florets (102) from all capitula (10) of one plant of *R. hirta* were sampled to determine the degree of variability in the percentage of the length of the ray floret reflecting ultraviolet light. This variability was found to be reasonably low (0.483 ± 0.0212 S.D. of all ray florets of 1 plant) making it possible to sample 1 ray floret/capitulum. These florets were collected and placed into glassine envelopes in the field, pressed, and dried. We sampled each population by collecting from 12 to 15 plants and collecting 1 ray floret/capitulum from 1 to 13 capitula. Thus, for each population a mean percent reflecting length was calculated for each plant and these means were then used to calculate a mean percent reflecting length for the local population.

The pattern of ultraviolet reflectance of the ray florets was determined by photographing the florets on 35 mm Kodak Plus-X film using a Kodak 18A filter (UV transmitting). Time exposures were used with an UV light source making it possible to use a regular glass camera lens. The exposed film was developed in Kodak D–19 developer (for high contrast) for 5 minutes at 20° C. The negatives were projected to twice life size and the total length and UV absorbing length of the ray floret were measured to the nearest mm. Because the border between the UV absorbing and UV reflecting portions of the florets is not a straight line, the center of the border was approximated for measurement. This UV reflectance pattern could also be determined using the simpler technique of Eisner *et al.* (1973) but with less precision than our method.

RESULTS

The mean fraction reflecting length of ray florets for each population is given in Table 1 and is shown graphically in Figure 1. *Rudbeckia triloba* had the smallest percentage of ultraviolet reflecting length (33%). *Rudbeckia hirta* was intermediate with 51%. *Rudbeckia laciniata* had the greatest percentage (83%) (see Figure 2). These differences are significant at the 0.001 level as tested by the Mann-Whitney one-tailed *U*-test. The intra-population variation was low in both *R. triloba* and *R. laciniata* but relatively high in *R. hirta*. The inter-population variation was low in *R. triloba* as well as in the Pennsylvania populations of *R. laciniata*. However, there was a marked difference between the Pennsylvania and Connecticut populations of *R. laciniata* ($p < 0.001$, Mann-Whitney one-tailed *U*-test) which increased the standard deviation for the species as a whole. We found more inter-population variation in the Connecticut populations (0.52 ± 0.054 S.D.) of *R. hirta* than in the Pennsylvania populations (0.506 ± 0.0253 S.D.). However, there was no significant difference between the mean of the Connecticut populations and the mean of the Pennsylvania populations.

The mean length of ray florets for each population is given in Table 1. *Rudbeckia triloba* had the shortest ray florets ($\bar{x} = 16.2$ mm) with both low intra-population and inter-population variation. *Rudbeckia hirta* had intermediate length ray florets ($\bar{x} = 25$ mm) with both relatively high intra-population and inter-popu-

Table 1. Means and standard deviations for fraction of UV reflecting length and total length of ray florets for populations of *Rudbeckia*.

Site	Locality (see Collection Data)	Species	N (plants)	*Reflecting length* Total length (± S.D. -plants)	Total length (mm)
1	PA	*R. hirta*	15	0.50 ± 0.067	27. ± 5.4
2	PA	*R. hirta*	14	0.54 ± 0.079	28. ± 4.3
3	PA	*R. hirta*	12	0.50 ± 0.054	23. ± 3.5
4	PA	*R. hirta*	12	0.48 ± 0.059	27. ± 3.1
5	CT	*R. hirta*	12	0.53 ± 0.073	20.0 ± 2.86
6	CT	*R. hirta*	12	0.47 ± 0.043	22. ± 3.1
7	CT	*R.hirta*	12	0.57 ± 0.050	29. ± 4.6
	R. hirta			0.51 ± 0.037 (± S.D. -populations)	25. ± 3.4
8	PA	*R. triloba*	12	0.314 ± 0.0166	14.7 ± 1.46
9	PA	*R. triloba*	12	0.37 ± 0.043	15.6 ± 1.96
10	PA	*R. triloba*	12	0.330 ± 0.0118	16.3 ± 0.56
11	PA	*R. triloba*	12	0.307 ± 0.0087	17.1 ± 1.49
12	PA	*R. triloba*	12	0.319 ± 0.0122	17.2 ± 0.99
	R. triloba			0.327 ± 0.0228	16.2 ± 1.05
13	PA	*R. laciniata*	12	0.829 ± 0.0256	39.3 ± 2.82
14	PA	*R. laciniata*	12	0.850 ± 0.0170	36. ± 4.2
15	PA	*R. laciniata*	12	0.880 ± 0.0159	34. ± 4.2
16	PA	*R. laciniata*	12	0.840 ± 0.0128	34. ± 4.4
17	CT	*R. laciniata*	12	0.725 ± 0.0228	31.1 ± 0.70
	R. laciniata			0.83 ± 0.059	35. ± 3.0

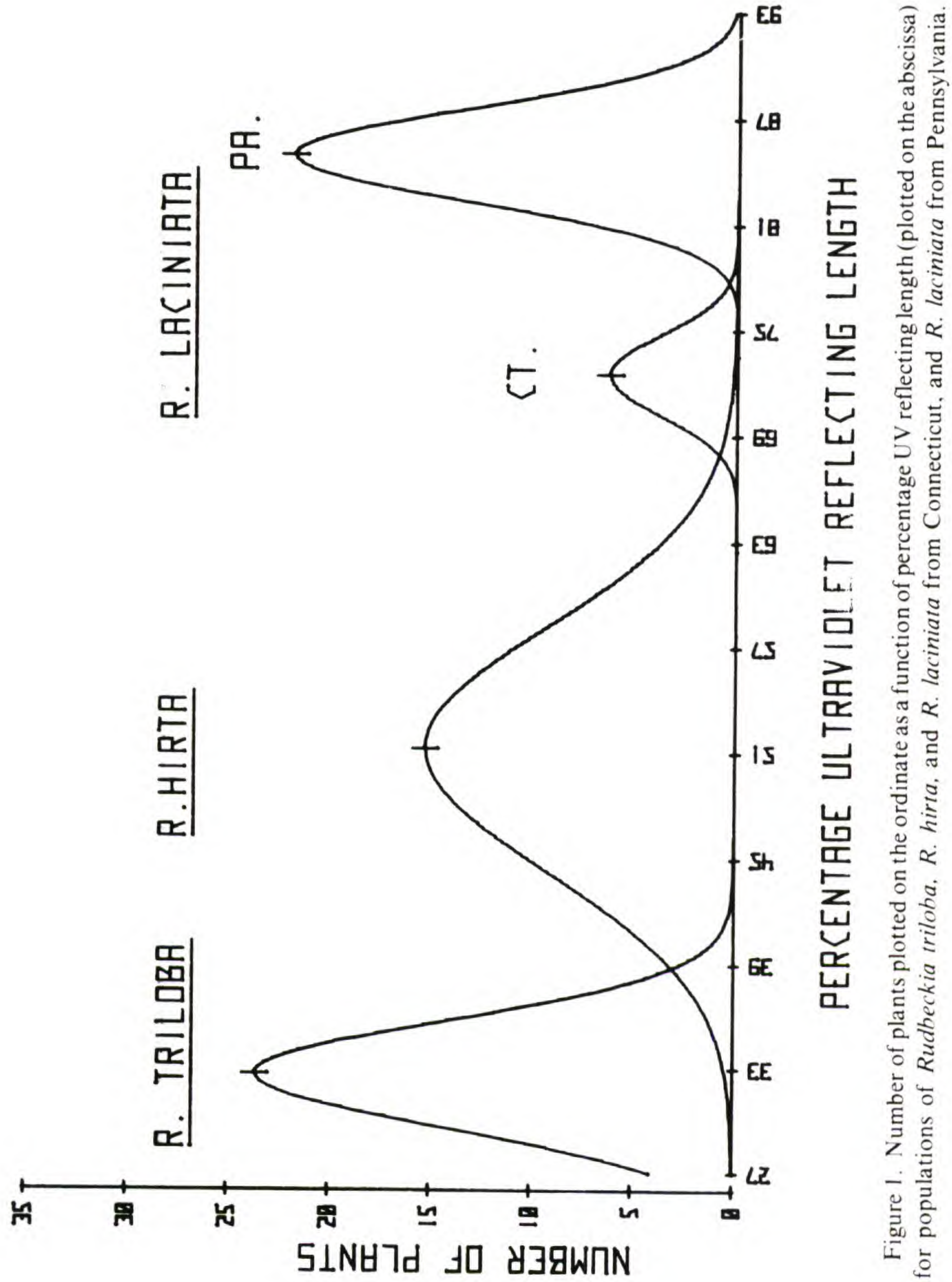

Figure 1. Number of plants plotted on the ordinate as a function of percentage UV reflecting length (plotted on the abscissa) for populations of *Rudbeckia triloba*, *R. hirta*, and *R. laciniata* from Connecticut, and *R. laciniata* from Pennsylvania.

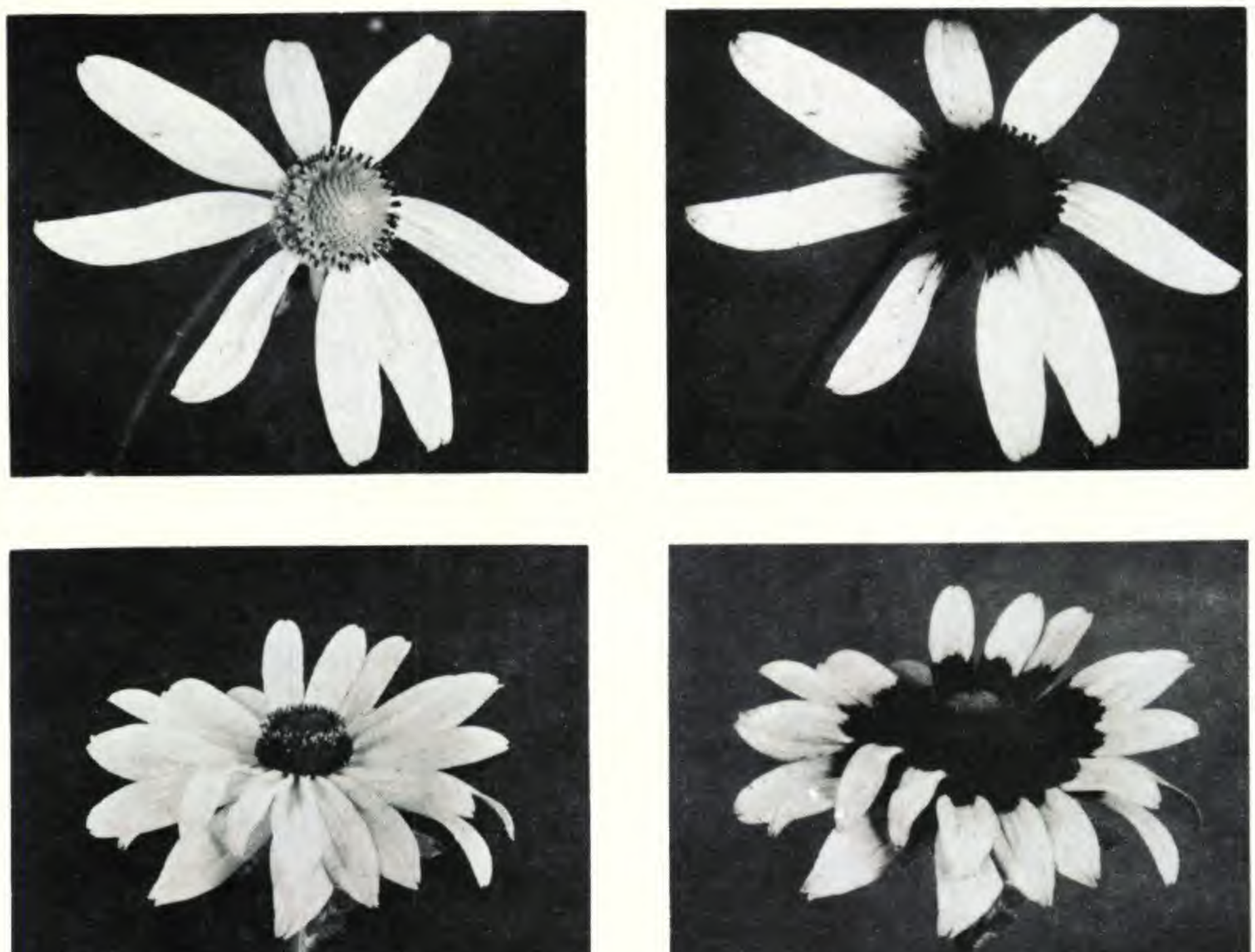

Figure 2. Visible and ultraviolet light reflection and absorption patterns in *Rudbeckia.* Top row, *R. laciniata:* left, visible light, right, UV light. Middle row, *R. hirta:* left, visible light, right, UV light. Bottom row, *R. triloba:* left, visible light, right, UV light. All shown at approximately the same scale.

lation variation. We found more inter-population variation in the Connecticut populations (24. ± 4.7 S.D.) of *R. hirta* than in the Pennsylvania populations (26.3 ± 2.22 S.D.). However, there was no significant difference between the mean of the Connecticut populations and the mean of the Pennsylvania populations. *Rudbeckia laciniata* had the largest ray florets ($\bar{x}$ = 35 mm) with both relatively high intra-population and inter-population variation. The Connecticut population was appreciably different from the Pennsylvania populations for this character.

We tested each population to see if the percentage of ultraviolet reflecting length was related to total length of the ray florets. No correlation was found within the populations. However, we did note a high correlation ($Y = 36.41X + 5.34$, $r = 0.94$, $N = 17$) between the percent reflecting length and total length of ray florets when using the means of all 17 *Rudbeckia* populations. It is evident that the lesser the population UV mean reflecting percentage, the shorter the population mean ray floret length.

DISCUSSION

Color vision in honeybees was demonstrated over sixty years ago (von Frisch, 1915) and the ability of honeybees to perceive ultraviolet light was shown by Hertz (1937a, b, c, 1939). A number of studies has now been made examining UV and color patterns of flowers (e.g. Richtmyer, 1923; Lutz, 1924, 1933; Lotmar, 1933; Mazokhin-Porshnyakov, 1959; Kevan, 1972; Horovitz & Cohen, 1972; Carter, 1974; Guldberg & Atsatt, 1975). We can assume that the various patterns are the result of coevolution of flower and pollinator. However, detailed studies of specific pollinator and flower UV pattern relationships are lacking. Thus it is only possible for us to state that we believe the differences between the three species of *Rudbeckia* are sufficient so as to allow pollinator discrimination, which is based in part on UV pattern.

Our finding of a significant correlation between population mean ultraviolet reflecting percentage and population mean ray floret length suggests a possible evolutionary trend to keep the "bull's-eye" of the capitulum at a relatively small UV absorbing size in the three species examined. Thus, even though the heads of *Rudbeckia laciniata* are large relative to the other two species examined, their UV absorbing "bull's-eye" remains small. However, this finding is not conclusive as many more species of *Rud-*

beckia would need to be examined for this character.

The basis of ultraviolet absorption in *Rudbeckia hirta* has been shown to be due to the presence of flavonol glucosides (Thompson *et al.*, 1972). Based on the similarity of colors and intensity of UV absorption of heads of *R. laciniata* and *R. triloba* to *R. hirta*, it is likely that similar flavonol glucosides are involved in these species as well.

This study further indicates the considerable taxonomic value of ultraviolet floral patterns (e.g., Carter, 1974). Correlation of breeding system with UV reflection should provide interesting results. For example, the limited intra-population variation in the UV nectar guide pattern in *Rudbeckia triloba* and *R. lanciniata* correlates with the apomictic breeding system of these two species (Gustafsson, 1947) and suggests a clonal origin of populations. The greater variation in the UV nectar guide pattern within populations of *Rudbeckia hirta*, an obligate outbreeder, probably indicates that there is only relatively weak stabilizing selection acting on the UV nectar guide pattern.

ACKNOWLEDGMENTS

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DEPARTMENT OF BIOLOGY
BUCKNELL UNIVERSITY
LEWISBURG, PENNSYLVANIA 17837

Present address, K. D. M.
DEPARTMENT OF BIOLOGICAL SCIENCES
PURDUE UNIVERSITY
WEST LAFAYETTE, INDIANA 47907

APPENDIX: COLLECTION DATA

Rudbeckia hirta

Sites

1 Pennsylvania, on Rte. 44, 2 miles W. of Oval, open field
2 Pennsylvania, Dale's Ridge Area near Lewisburg, open field

3 Pennsylvania, Dale's Ridge Area near Lewisburg, open field
4 Pennsylvania, Dale's Ridge Area near Lewisburg, open field
5 Connecticut, Mt. Carmel Ave., 0.3 mile E. of Rte. 10, Hamden, shaded roadside
6 Connecticut, Brewster Lane, No. Haven, open field
7 Connecticut, Spruce Bank Road, Hamden, open field

Rudbeckia triloba

Sites

8 Pennsylvania, on Rte. 45, 0.5 mile E. of Montandon, open field
9 Pennsylvania, Covered Bridge at Chillisquaque Creek, 2 miles E. of Montandon, partly shaded
10 Pennsylvania, 1 mile SE. of Montandon, open roadside
11 Pennsylvania, 0.1 mile N. of Rte. 192 in Cowan, partial shade
12 Pennsylvania, 0.5 mile N. of Cowan on Shinbone Road, open field

Rudbeckia laciniata

Sites

13 Pennsylvania, River Road, 0.8 mile south of Lewisburg, open
14 Pennsylvania, Covered Bridge at Chillisquaque Creek, 2 miles E. of Montandon, shaded
15 Pennsylvania, 0.1 mile N. of Rte. 192 in Cowan, shaded
16 Pennsylvania, 0.6 mile W. of Cowan on Rte. 192, partial shade
17 Connecticut, Mansfield Road, No. Haven, open

THE POLLINATION ECOLOGY OF A POPULATION OF ERYTHRONIUM AMERICANUM KER. (LILIACEAE)

PETER BERNHARDT

There are considerable gaps in our knowledge of the complete life history of the indigenous species of vernal flowering herbaceous angiosperms. The anecdotal information presented in local flora guides is an aid to the identification of populations, but it does not always help us to appreciate the evolutionary significance of floral and vegetative modifications. Nor can it explain the subtle interactions between one species and other plant and animal populations within the vernal community.

While the vegetative propagation of *Erythronium americanum* has been well documented (Gleason & Cronquist, 1963), floral reproduction has been poorly recorded. Does the pollination of the flower lead to the production of fruit and seed in this species? How is the transmission of the pollen effected? Work done on the pollination ecology of several vernal species has shown that a variety of reproductive strategies may be employed under surprisingly similar restrictive environmental conditions (Proctor & Yeo, 1972).

The phenology and anatomy of *Erythronium americanum* flowers suggest pollination by insect vectors. The bright yellow perianth displays the bell/ funnel form (Faegri & van der Pijl, 1971) while the nodding peduncle would restrict foraging to vectors that could feed while hovering or by clinging in an inverted position. Macior (1966, 1970) has found that Hymenoptera active at this time of year are capable of the latter style of feeding and pollination.

The study reported here had two objectives. First, using experimental methods in the field, it sought to determine the mode or modes of floral reproduction that lead to the development of seed and fruit. Second, it sought to identify the vectors (if any) of pollination.

STUDY SITE AND STUDY POPULATION

The population of *Erythronium americanum* studied is located in Swartout's Woods of the State University College at Brockport campus, in the town of Sweden, the village of Brockport in Monroe County, New York. The forest canopy consists of mature silver

maple mixed with beech saplings. Anthesis of *Erythronium americanum* overlapped the anthesis of local populations of *Trillium grandiflorum* (Michx.) Salisb., *Hepatica acutiloba* DC., *Dicentra cucullaria* (L.) Bernh., *Dentaria laciniata* Muhl., *Trillium erectum* L. and *Caulophyllum thalictroides* L. Flowers of *Erythronium americanum* began to bloom on April 25, 1975, and withered entirely by May 10, 1975.

PROCEDURE

The field study was begun on April 20, 1975, and was concluded on May 25, 1975. Just prior to blooming, sixty flower buds were chosen at random over the entire colony. Each bud selected was placed in a transparent plastic bag and sealed with thread. Following the opening of the perianth, fifteen blossoms were placed in each of four experimental categories listed and defined below.

Controls: Following the onset of anthesis, the bag was removed. Fruit produced in this category should give a normal indication of the rate of fruit production in the population.

Emasculates: Following the onset of anthesis, the bag was removed and the anthers excised. If fruit is produced in this category, fertilization is initiated by foreign pollen that must be transmitted by a vector.

Isolates: Following the onset of anthesis, the bag was not removed. If those flowers that are denied access to foreign pollen set fruit, then fertilization is via self-pollination.

Isolated Emasculates: Following the onset of anthesis, the bag was removed, the anthers excised, and the bag was replaced and resealed. Blossoms that set fruit in the absence of pollen are apomictic.

Insect activity was noted in the field during morning, afternoon and evening periods. Insects were caught selectively when they were observed either clinging on the floral parts or actively foraging for floral nutrients on open flowers of *Erythronium americanum*. Each insect was placed in a separate vial containing 75% ethanol and examined for the presence of the host plant's pollen. Insects were keyed to species when possible.

On May 24, 1975 the flowers belonging to the four categories were harvested and checked for the presence of fruit and seed.

OBSERVATIONS

Those flowers that belonged to the two artificially isolated categories failed to set fruit (Table 1). Apparently, this species is self-incompatible and, since only the Emasculates approach the fruit production of the Controls, we may assume that *Erythronium americanum* is an obligate out-crosser.

Foragers carrying depositions of the host plant's pollen were collected during morning and afternoon periods as the perianths closed at dusk. One species of Coleoptera and six genera of Hymenoptera were found carrying *Erythronium americanum* pollen. All foragers fed while clinging to the floral parts. Feeding while hovering was never observed.

Individuals of *Asclera ruficollis* (Say) were found bearing a fine dusting of pollen on both the ventral and dorsal sides of the head, thorax, abdomen and legs. They were taken while they fed on the anthers or chewed on the stigma.

Pollen on all Hymenoptera was confined to the ventral side of the head, thorax and abdomen or deposited in the corbicular load. The only *Bombus bimaculatus* Cresson queen taken bearing a mixed load of host flower pollen and the pollen of another species bore the pollen of *Dicentra cucullaria* in her corbicular basket. *Nomada sulphurata* Sm. carried depositions of *Dentaria laciniata* pollen only. All *Andrena* spp. carried mixed loads, the *Nomada* sp. near *dentariae* Robt. and the *Nomada* sp. carried depositions of host plant pollen and the pollen of *Dentaria laciniata* (Table 2).

DISCUSSION

There is a significant drop between fruit production in Controls and Emasculates. I suspect that insects primarily concerned with the collection and consumption of *Erythronium americanum* pollen spent less time on the Emasculates, which did not allow sufficient time for the ventrally distributed pollen to be passed to the inverted stigma. Unlike *Asarum canadense* L., which displays floristic modifications for self-pollination (Wildman, 1950), and *Viola* spp., which are self-pollinated by insects (Beattie, 1971), *Erythronium americanum* appears to be one vernal species that relies on outcrossing for the production of seed.

Since *Apis mellifera* L. is not native to North America, we must conclude that pollination by this insect is a preadaptive process between an introduced vector and an indigenous plant. Also,

Table 1. **Flower vs. fruit production in Erythronium americanum.**

CATEGORY	Number of flowers tested	Number of withered flowers recovered	Number of flowers with fruit
CONTROLS	15	11	10
EMASCULATES	15	15	12
ISOLATES	15	12	0
ISO. EMASC.	15	11	0

Table 2. **Insect foragers on Erythronium americanum and the pollen carried.**

INSECT SPECIES	*Analysis of pollen carried by foragers* host only	host & other spp.	other spp. only	no pollen
COLEOPTERA:				
Asclera ruficollis	6	0	0	0
DIPTERA:				
Polenia rudis	0	0	0	1
HYMENOPTERA:				
Andrena carlini	0	4	0	0
Andrena spp.	2	3	0	1
Apis mellifera (workers)	3	0	0	0
Bombus bimaculatus (queens)	4	1	0	0
Dialictus coerulus	1	0	0	0
Nomada sp.	0	1	0	0
Nomada sp. (near *dentariae*)	1	1	0	0
Nomada sulphurata	0	0	1	0
Osmia atriventris	1	0	0	0
TOTALS	18	10	1	2

unlike vernal species like *Dicentra cucullaria,* anatomical modifications of the floral parts in *Erythronium americanum* do not appear to restrict pollination to a finite group of correspondingly modified vectors that belong to the same tribe, genus or species as in the former (Macior, 1970). Unlike vernal flowering populations of *Viola, Physalis, Salix, Polemonium reptans,* and *Claytonia virginica, Erythronium americanum* does not appear to be a major pollen source for entirely oligolectic species of solitary bees as described by Linsley (1958).

SUMMARY

Under experimental conditions, seed production in *Erythronium americanum* is entirely the result of outcrossing. Artificially isolated blossoms appear to be self-incompatible. Cross-pollination is effected by insects that forage by clinging to the floral parts rather than by hovering. Foragers bearing the host plant's pollen include *Asclera ruficollis, Apis mellifera* and indigenous populations of social and solitary bees. *Erythronium americanum* appears to share some vectors with colonies of vernal herbs with overlapping periods of anthesis as some insects collected on the host flower bore the pollen of two other species.

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PRELIMINARY NOTES ON THE STRUCTURE OF STIGMATIC SURFACES IN THE BEGONIACEAE

A. I. BARANOV

In the botanical literature to date, very little or nothing has been said about the micro-structure of the stigmatic surfaces in the Begoniaceae. However, my recent studies of the gross morphology of *Begonia* flowers have shown that these surfaces have a varied morphological structure in different members of this family. The following initial observations are offered as a preliminary contribution to the study of this situation.

MATERIALS AND METHODS

Stigmatic surfaces of twenty-five taxa are noted in this article. The main portion of this group consists of twenty-three species of *Begonia* belonging to sixteen sections. These plants are noteworthy for their rarity but are currently cultivated in greenhouses in the Boston area. Results of the study of stigmatic surfaces of *Begonia roxburghii* A.DC. (sect. *Sphenanthera*) were added to the results of the study of the twenty-three previously mentioned *Begonia* species.

Begonia flowers collected in greenhouses were immediately fixed in 70 per cent alcohol. The fixed material was dissected, studied in the laboratory with the help of a dissecting stereo microscope, and subsequent drawings were made.

Wild or native plant material of *Hillebrandia sandwicensis* Oliver was studied by the same method. The flowers of this plant, fixed in 70 per cent alcohol with a few drops of glycerin, were received from Dr. Derral Herbst (Harold L. Lyon Arboretum, University of Hawaii at Manoa, Honolulu, Hawaii). The voucher specimen for the fixed material, *Herbst 5302,* has been deposited in the Herbarium of the Arnold Arboretum.

MORPHOLOGICAL TYPES OF STIGMATIC SURFACES

The structure of a stigmatic surface in each species studied has been carefully checked and sketched (Plate I). I have found that this structure differs significantly among various taxa of the


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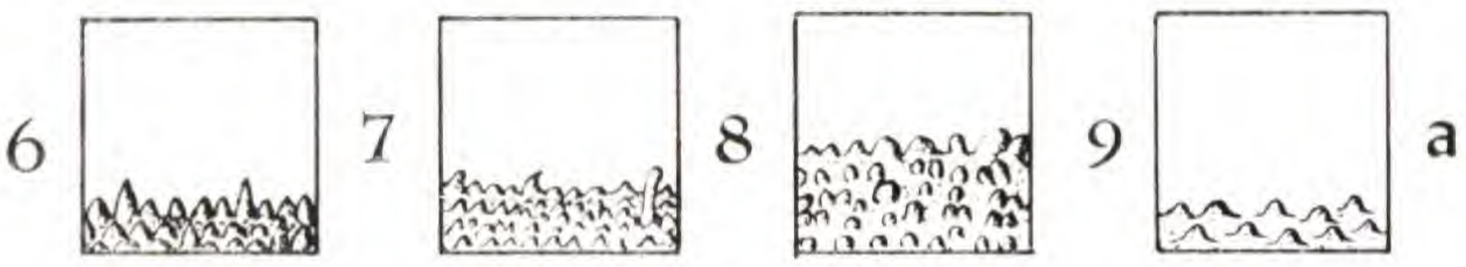
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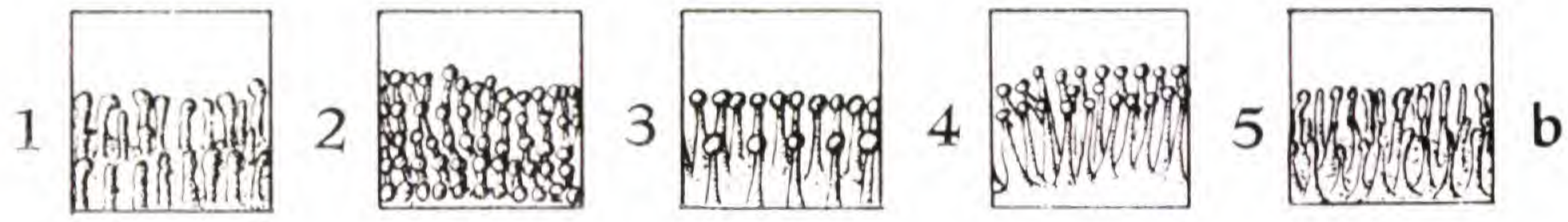
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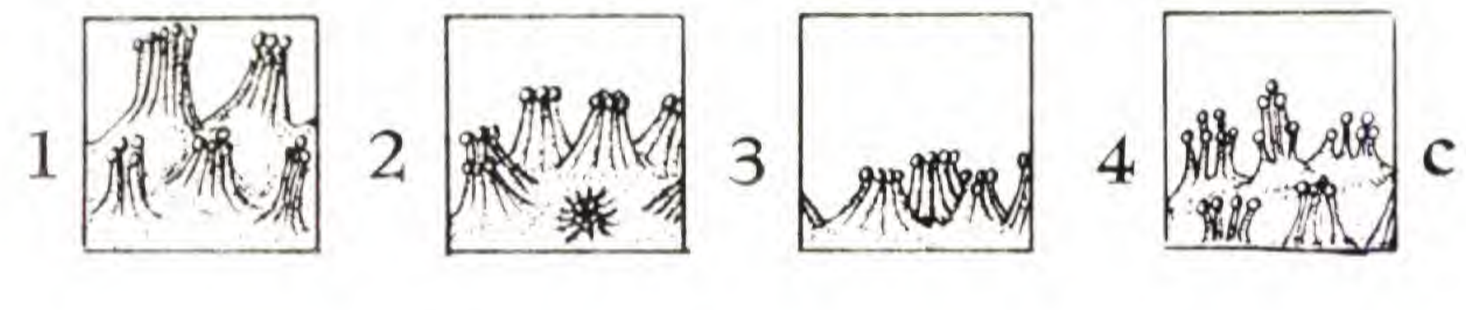
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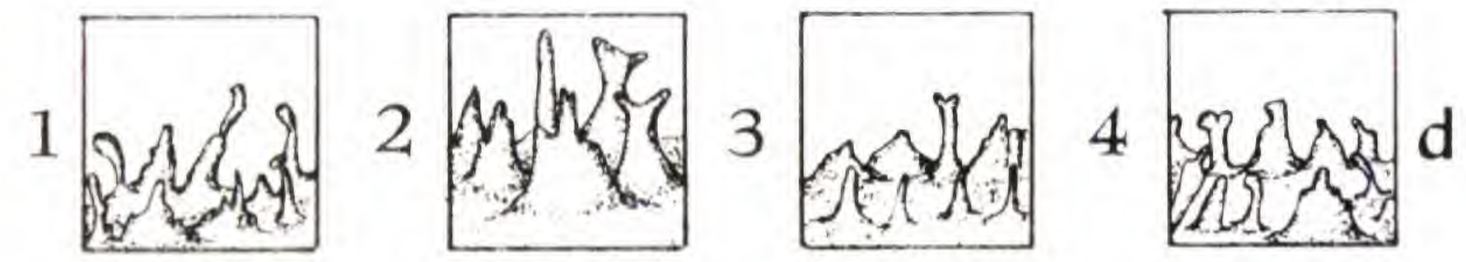
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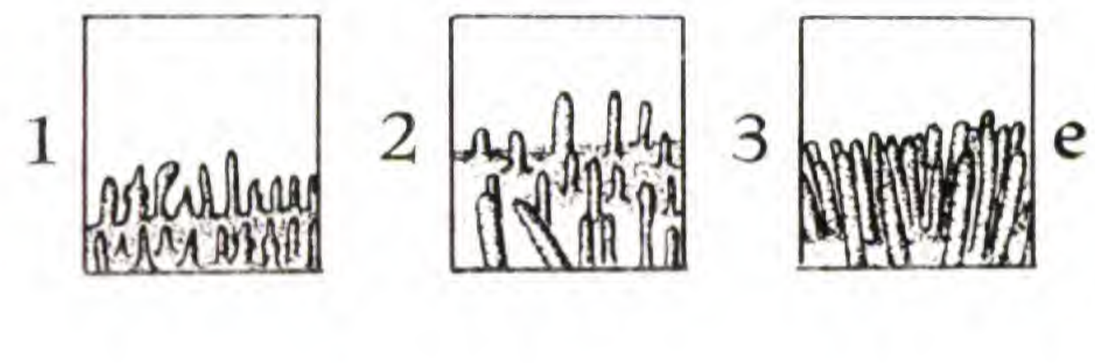
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Begoniaceae. The selected twenty-five species have the following types of stigmatic surfaces which can be arranged in five groups.

Group *a*. Stigmatic surfaces covered with wart-like, low conical, papillose or nipple-like, fleshy excrescences (9 species).
Group *b*. Stigmatic surfaces covered with capitate, glandular hairs (5 species).
Group *c*. Same as above, but the capitate, glandular hairs are densely packed into conical, pyramid-like piles (4 species).
Group *d*. Stigmatic surfaces covered with irregularly shaped, fleshy, pinnacle-like excrescences (4 species).
Group *e*. Stigmatic surfaces covered with fleshy, rod-like excrescences (3 species).

Each of the five types is not restricted to any particular section. Plants from different sections, and even genera, can belong to the same grouping. For example, Group *a* is formed by plants from *Begonia* and *Hillebrandia,* and the *Begonia* species are from six different sections.

There is a certain degree of variation in the structure of stigmatic excrescences, not only among the separate groups, but also

PLATE I. LEGEND

Plate I. Semi-diagrammatic figures of portions of stigmatic surfaces in different members of the Begoniaceae. Each Figure at × 60. *a,* Tubercled, papillose or nipple-like excrescences, figures 1–9. 1, *Hillebrandia sandwicensis* Oliver; 2, *Begonia roxburghii* A.DC (Sphenanthera); 3, *Begonia fuchsiaeflora* A.DC (Casparya); 4, *Begonia convolvulacea* A.DC (Enita); 5, *Begonia monophylla* Pavon ex A.DC (Huszia); 6, *Begonia acida* Vellozo (Pritzelia); 7, *Begonia echinosepala* Regel (Pritzelia); 8, *Begonia vitifolia* Schott in Spr. (Pritzelia); 9, *Begonia floccifera* Beddome (Reichenheimia). *b,* Capitate, glandular hairs, figures 1–5. 1, *Begonia egregia* N.E. Brown (Tetrachia); 2, *Begonia herbacea* Vellozo (Trachelocarpus); 3, *Begonia boisiana* Gagnep. (Petermannia); 4, *Begonia foliosa* H.B.K. (Lepsia); 5, *Begonia franconis* Liebm. (Doratometra). *c,* Capitate, glandular hairs densely packed into piles, figures 1–4. 1, *Begonia pustulata* Liebm. (Weilbachia); 2, *Begonia goegoensis* N.E. Brown (Reichenheimia); 3, *Begonia schmidtiana* Regel (Begonia); 4, *Begonia cucullata* Willd. var. *hookeri* Smith & Schub. (Begonia). *d.* Irregularly shaped, pinnacle-like excrescences, figures 1–4. 1, *Begonia boliviensis* A.DC (Barya); 2, *Begonia dipetala* R. Graham in Hooker (Haagea); 3, *Begonia sudjanae* Jannson (Reichenheimia); 4, *Begonia mannii* Hook. f. (Tetraphila). *e,* Rod-like excrescences, figures 1–3. 1, *Begonia epipsila* Brade (Pritzelia); 2, *Begonia maculata* Raddi (Gaerdtia); 3, *Begonia pseudo-lubbersii* Brade (Begonia).

within each one of the groups (Plate I). For example, in Group *a* the excrescences may be low, with a rugged outline (*Begonia roxburghii* A.DC, Plate I, Figure 2a), or they may be conical and smooth (*B. convolvulacea* A.DC, Plate I, Figure 4a and *B. monophylla* Pavon ex A.DC, Plate I, Figure 5a). In certain cases excrescences may be elongated (*B. fuchsiaeflora* A.DC, Plate I, Figure 3a), or wart-like, rounded (*B. vitifolia* Schott in Spr., Plate I, Figure 8a).

In the first, second and fifth groups it appears that transitional forms of stigmatic excrescences can be detected. For example, in *Begonia echinosepala* Regel (Plate I, Figure 7a) some of the excrescences tend to attain a rod-like form although the majority of them are conical and papillose. In *B. franconis* Liebm. (Plate I, Figure 5b) stigmatic excrescences have an intermediate shape between rod-like and capitate hair-like forms, and in *B. epipsila* Brade (Plate I, Figure 1e) some of the excrescences tend to attain either a nipple-like or an irregular, pinnacle-like shape, although the majority of them seem to be rod-like.

CONCLUSION

My observations on the morphology of stigmatic surfaces in the Begoniaceae indicate that much work remains to be done to complete this study. The observations described in preceding paragraphs have been made on a very small scale, with meager materials and with some very simple equipment. Understandably, the results of this study must be verified. Further study of the types of excrescences on stigmatic surfaces of the Begoniaceae must be carried out with the help of better instruments and on a larger scale. As many species and genera as possible should be covered by a follow-up study. Furthermore, it might be expedient to begin the study of the developmental patterns of the stigmatic surfaces in different species and genera of the Begoniaceae.

An additional and very interesting topic related to this research project might be the study of stigmatic surfaces in *Begonia* hybrids in order to discover whether their stigmatic surfaces display a combination of traits of parent species or if they follow the structural pattern of one of the parent taxa. The real turning point in morphological study of the stigmatic surfaces in the Begoniaceae will be their study and photographing with the help of a scanning microscope. Only by such a study will these structures be well documented, and their taxonomic value, if any, be discovered.

ACKNOWLEDGMENTS

The writer is grateful to the staff of the Northeastern University Greenhouses, Woburn, Massachusetts, and to Mr. Michael Kartuz, owner of the Kartuz Greenhouses, Wilmington, Massachusetts, for their willingness to supply him with *Begonia* flower material. Special acknowledgment is due to Dr. Derral Herbst of Honolulu, Hawaii for a collection of *Hillebrandia* flowers provided specially for this study. Furthermore, the author is grateful for access to the Arnold Arboretum-Gray Herbarium Library where he was able to consult literature necessary for the preparation of this study.

14 EGMONT STREET
APT. #6
BROOKLINE, MA 02146

TYPIFICATION OF TIQUILIA DARWINII AND TIQUILIA FUSCA (BORAGINACEAE)

DUNCAN M. PORTER

The genus *Galapagoa* Hooker f. was published by Joseph Hooker in 1847. Hooker considered the genus to be endemic to the Galápagos Islands. In 1862, Asa Gray, recognizing their affinities with species in *Coldenia* L., transferred Hooker's two species to that genus. In 1937, John Thomas Howell, in a paper on the Galápagos coldenias, typified Hooker's names and described two new species. More recently, Richardson (1976) has recognized that *Coldenia* should be restricted to one species of southern Asia, and accordingly transferred those New World species hitherto included in *Coldenia* to *Tiquilia* Persoon. The purpose of this paper is to discuss Howell's typification of Hooker's two Galápagos species, the types of which Richardson did not see during the preparation of his monograph.

Tiquilia darwinii (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Galapagoa darwinii Hooker f., Trans. Linn. Soc. London **20:** 196. 1847.
Coldenia darwinii (Hooker f.) A. Gray, Proc. Am. Acad. Arts **5:** 341. 1862.

TYPE: "Chatham Island, *Charles Darwin, Esq.* Albemarle Island, *Mr. Macrae.*"

SPECIMENS EXAMINED: *Darwin,* Sept. 1835, Chatham Island (CGE, Mus. Henslow., here chosen as lectotype); *Macrae,* Albemarle Islds. (CGE, Herb. Lemann, syntype); *Macrae,* Albemarle Island (CGE, syntype); *Macrae,* Albemarle Isld. (K, Herb. Hook., syntype); *McRae,* Albemarle islds. (K, Herb. Hook., syntype); *Macrae,* Ins. Albemarle Gallipagorum (K, Herb. Benth., syntype).

Typification of this and the following species was misinterpreted by Howell (1937), and in turn the two species have been misinterpreted. Like many taxonomists before and since, Howell apparently thought that the first set of Darwin's Galápagos collections was at Kew and chose lectotypes accordingly. However, the first set is at Cambridge, those specimens at Kew being duplicates.

In attempting to typify this species, Howell, after examination of the Darwin and Macrae collections at Kew and Cambridge,

chose a Darwin specimen at Kew from Charles Island as the lectotype for this taxon: "For the type of the species, there should be no hesitancy in choosing Darwin's specimens in Herb. Hook. because (1.) the material is adequately covered by the original description of *G. darwinii* and is clearly included in Hooker's drawings of dissections; (2.) it is the first cited collection; (3.) the species named after Darwin should have as the type this specimen collected by him, if his plant is included in the original description. This decision is reached and held in spite of the fact that Darwin's collection in Herb. Hook. is labeled 'Charles Island,' while the island named both in the original description and in the data accompanying the specimen in Herb. Cantab. [CGE] is Chatham Island; and also in spite of the fact that the specimen from Charles Island by Darwin in Herb. Benth., which is labelled *G. darwinii,* is *C. fusca* and exactly corresponds to Edmonston's plant from Charles Island in Herb. Hook." (Howell, 1937, p. 101). The Edmonston collection is mounted on the same sheet as Howell's lectotype.

The specimens cited above under "specimens examined," being syntypes of *Galapagoa darwinii,* are the only ones available to serve as lectotypes, notwithstanding Howell's interpretation of Hooker's type description. Darwin's Chatham Island collection *does* fit Hooker's description of this taxon, as do the Macrae collections. Presumably, Howell thought the type should be at Kew, and no Chatham Island collection being there, a Charles Island collection was chosen. Today, his second and third reasons should not enter into lectotype selection (International Code of Botanical Nomenclature, "Guide for the determination of types," Note 4).

In addition, Hooker's drawings may or may not be attached to the specimens from which they were made. For example, his drawing of *Galapagoa fusca* at Kew is attached to *Andersson 175,* collected in 1852. Hooker's drawing of *G. darwinii* is attached to a Macrae collection which Howell chose as the lectotype of *Coldenia fusca!*

Tiquilia fusca (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Galapagoa fusca Hooker f., Trans. Linn. Soc. London **20:** 197. 1847.

Coldenia fusca (Hooker f.) A. Gray, Proc. Am. Acad. Arts **5:** 341. 1862.

TYPE: "Charles Island, *Charles Darwin, Esq.*"

SPECIMENS EXAMINED: *Darwin,* Sept. 1835, Charles Island

(CGE, Mus. Henslow., holotype); *Darwin,* end of Sept. 1835, Charles Island (K, Herb. Hook., isotype); *Darwin,* end of Sept. 1835, Charles Island, (K, Herb. Benth., isotype).

Misinterpretation of this species and the preceding was caused, in part, by Howell's (1937) lectotypification of *Coldenia darwinii* by the Herb. Hook. isotype of *C. fusca.* In turn, he typified *Coldenia fusca* by a syntype of *C. darwinii* [*Macrae,* Albemarle Island (K, Herb. Hook.)], all contrary to the International Code of Botanical Nomenclature. Howell chose this Macrae specimen because the Darwin collections (except for the Herb. Benth. specimen from Charles Island) already had been ascribed by him to *Coldenia darwinii.* Darwin's Herb. Benth. specimen was not indicated as a type, because Howell doubted that it had been collected on Charles Island. Whether it had been or not is beside the point; it was labeled as such by Hooker and cited as such by him in the protologue. Darwin's Charles Island specimens are the only ones that can serve for typification, and indeed they do fit Hooker's description.

This misinterpretation has led to Galápagos collections of *Tiquilia darwinii* to be determined as *T. fusca,* and vice versa, using the keys of Howell (1937) and Wiggins and Porter (1971).

ACKNOWLEDGMENTS

Herbarium studies were accomplished under a grant from the Penrose Fund of the American Philosophical Society to examine Charles Darwin's Galápagos collections at the Royal Botanic Gardens, Kew, and at the Botany School, Cambridge University. A paper discussing these collections is in preparation. The assistance of the Society and of the curators and staffs of these herbaria is gratefully acknowledged, as are the comments of my colleague Richard Mayes.

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DEPARTMENT OF BIOLOGY
VIRGINIA POLYTECHNIC INSTITUTE & STATE UNIVERSITY
BLACKSBURG, VIRGINIA 24061

A CRUSTOSE SPHACELARIOID NEW TO NORTHEASTERN NORTH AMERICA: BATTERSIA MIRABILIS

R. T. WILCE AND WALTER GROCKI

Until recently, the alga *Battersia mirabilis* Reinke ex Batters was known only from the original collections from Berwick-on-Tweed on the southeast coast of Scotland, made nearly a century ago, and from a single collection near Ladehammeren, Norway (Printz, 1926). It is now also known from the Dutch coast (Prud' Homme Van Reine, 1974) and from several localities in the southern Gulf of Maine between Rocky Point and Manomet Point, Massachusetts. Owing to the apparent rarity of the species and to its widely disjunct distribution, the Massachusetts plants of *Battersia* are here described and compared with the published descriptions and several specimens of European origin.

Battersia mirabilis came to our attention after careful collecting using SCUBA diving equipment and detailed laboratory analysis of samples of the numerous fleshy, brown crustose forms which occur in the algal flora of Massachusetts. At first, a curious ralfsioid crust with erect, short stalked, branched or simple, reproductive axes was observed. Upon closer inspection several characteristics readily distinguished it as a little-known component of the *Sphacelariales,* and later, with more material and study, the little sphacelarioid of Batters (1889), *Battersia mirabilis,* was identified.

Battersia mirabilis seems to be uncommon where it has been found, both in Europe and along the Massachusetts coast. Its occurrence is probably more frequent however, since the diminutive size of the crust (usually less than 1–2 cm. diameter) makes it easy to overlook or to confuse with the juvenile stages of several commonly associated brown crusts. Our knowledge of the species' seemingly preferred habitat, its morphology and the color of the living plant may, in time, aid in the recognition of this species as a more common element of the Massachusetts benthic algal flora.

The morphological uniqueness of this sphacelarian has brought *Battersia mirabilis* considerable attention from both Reinke (1891) and Sauvageau (1900). Both studies supplement the original de-

scription of the species by Batters (1889) and attempt to clarify the evolutionary position of the species within the *Sphacelariales.* Dried specimens and the alcohol preserved plants from the original collections of Batters (*leg.* January-February 1888 and October 1889) were the only material available to Reinke and later, Sauvageau.

Subsequent references to this species, prior to those of Prud' Homme Van Reine (1974), are those of Fritsch (1945), Newton (1931) and Parke and Dixon (1968); all refer to the original collections of Batters.

Specimen citation. *Battersia mirabilis,* Berwick-on-Tweed, Scotland, October 1889, *E. Batters.* A single large fragment of this collection is present in the Farlow Herbarium, Harvard University. The specimen was given to E. M. Holmes who included it in his Exsiccatae of "Algae Britannicae Rariores," #105, Fasciculus V, London, 1890. The Farlow Herbarium plant is reproductive, with numerous erect branching axes bearing unilocular sporangia, and is morphologically similar to plants of this species collected from the Massachusetts coast. The plant portions shown in Figure II represent various aspects of the specimen collected from the type locality by Batters.

The plant sent to Dr. W. G. Farlow (probably in the late 1890's) consisted of one large (3–4 cm. diameter at its maximum) fragment of a thick, dark-brown crust; branched reproductive axes bearing numerous unilocular sporangia are abundant on the surface of much of this fragment. All of the sporangia that we have seen from this specimen were devoid of spores or of cellular content.

Vegetative plant body. The vegetative portion of *Battersia mirabilis* consists of one to six overlapping and ultimately stratified layers, each of which in all probability consists of a single plant. Prud'Homme Van Reine (1974) describes both discoidal and filamentous germlings arising from zoospores and developing into mature crusts. Crusts are irregular in outline; 3.0–5.0 cm. in diameter; the upper surface uneven, appearing rough owing to the frequency of overlapping crust lobes, the appearance of the reproductive sori, numerous epiphytic algae, and an abundance of fine detrital sediments. The appearance of the crust in the field is clearly ralfsioid. Without optics, vegetative plants of *B. mirabilis* are virtually impossible to distinguish from such species as

Ralfsia verrucosa (Aresch.) J. Agardh, *Sorapion kjellmani* (Wille) Rosenv. and *Symphyocarpus strangulans* Rosenv.

Crust height is 3–15 cells (100–150μm.); the width of the basal cells range from 25–50μm. (35μm.), while the terminal cell of each filament is considerably smaller, 6.0–18μm. (14μm.), (Figure I). In this respect the crust of *Battersia* resembles *Sorapion kjellmani, S. simulans* Kuckuck and *Symphyocarpus strangulans* and differs dramatically from the structure of most other fleshy brown crustose taxa in the North Atlantic.

Plants of *Battersia mirabilis* are easily removed from rock substratum as large fragments. Crust texture is friable rather than of soft consistency as in *Petroderma maculiforme* (Wollny) Kuckuck, *Pseudolithoderma paradoxicum* Sears & Wilce and *Symphyocarpus strangulans.* Both the upper and lower crust surfaces show parallel cell rows and the rows are frequently arranged in small fan-shaped aggregates. With the aid of a dissecting microscope another distinctive vegetative feature is revealed in the larger than usual diameter (for brown crusts) of many surface cells. The diameter of surface cells and their arrangement in parallel rows or into fan-shaped clusters are of diagnostic value in determining the identity of vegetative plants to this genus.

Cytology. All cells of the crusts of *Battersia mirabilis* contain numerous discoidal plastids which do not appear to have pyrenoids as seen with the aid of the light microscope. Plastids are numerous in mature cells, ranging from 3.5–5.0 μm. diameter. Numerous small vesicles that we have interpreted as fucosan vesicles are present in developing unilocular sporangia and in the vegetative cells supporting the sporangia. In preserved material these vesicles aggregate to form a conspicuous dense mass (Figure I). The cell wall adjacent to the substratum is thickened owing to an outer, slightly pigmented layer in contact with the substratum. The material of this outer wall is yellowish to slightly amber in color. It is either an integral part of the cell wall or is secreted by the protoplast of the basal cells, and may function as a cementing substance.

Reproductive structures. With the aid of a dissecting microscope the crust surface may appear locally crowded with numerous, small, emergent filaments that bear reproductive organs (Figure I). Under higher magnification the filaments are seen to terminate

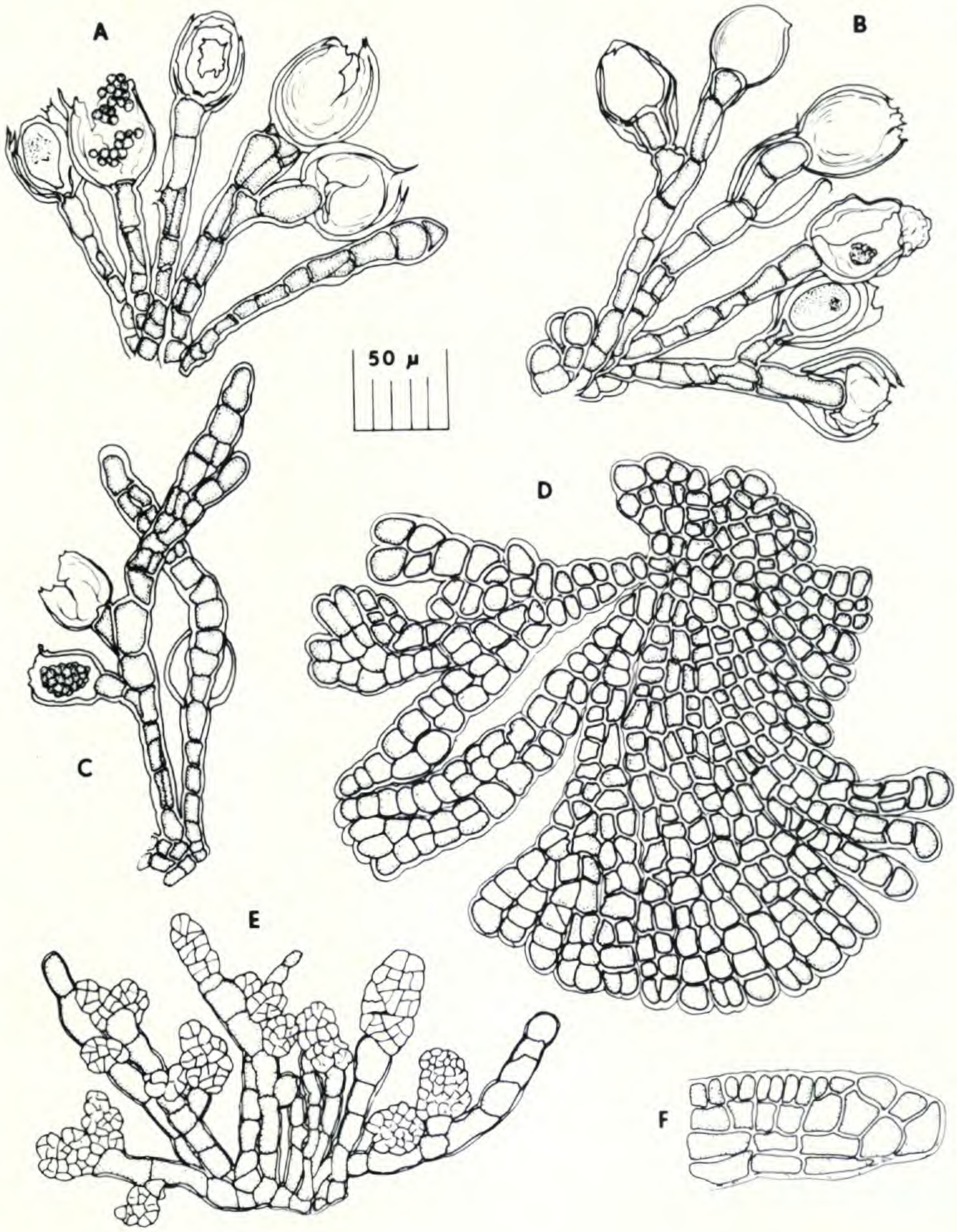

Figure I. Morphological features of plants collected from Manomet Point, Massachusetts: A–C, details of unilocular sporangia and their supporting axes; D, F, different views of the crustose plant; E represents axes bearing plurilocular reproductive organs.

in a vegetative apical cell, a generally globose sporangium, or in a plurilocular reproductive organ; the majority terminate in reproductive organs. The erect filaments of *Battersia,* unlike those of most sphacelarioids, contain cells which do not divide into superior and inferior secondary segments. Some axial cells, however, divide periclinally, resulting in a slightly parenchymatous axis, but these divisions are few. All cells of the erect axes have the potential of initiating lateral development of sessile or short, branch-supported reproductive organs.

Our *Battersia mirabilis* collections of February and May, 1975, include crusts with both unilocular and plurilocular sporangia, the latter newly described for this species. Collections through the summer and autumn, 1975, show only vegetative crusts. Mature sporangia are up to 40 μm. wide, 49 μm. long and are similar to those described by Batters (1889). The width of the cells subtending unilocular sporangia is 13–24 μm. (19 μm.), and the width of the third cell below the supporting cell is from 9–18 μm. (13 μm.). All of the mature reproductive axes that we have seen show a marked basipetal tapering. The plurilocular reproductive organs occur infrequently in our collections. They always occur on separate erect axes from those bearing the unilocular sporangia and may occur singly, terminating an axis, or several short-stalked or sessile sporangia may occur on a single axis. Plurilocular reproductive organs were present in the February collections and present but mostly discharged in the May, 1975, collections.

Propagules have not been recorded for this species and were not present in the Massachusetts collections.

Discussion. Owing to the combination of several characters, *Battersia mirabilis* is clearly sphacelarian. Cytologically it is identical with all of the described species in the *Sphacelariales.* Crust development is thoroughly described by Sauvageau (1900) and compared by him to a similar crust development in plants of *Ralfsia* and *Aglozonia.* Crust structure is filamentous, with lateral growth from marginal initials and growth in height from the divisions of terminal cells. Apical growth and subsequent longitudinal (periclinal) divisions of axial cells, common to most members of this order, occur in *Battersia,* but only in the cells of the upright axes. However, these cells like those of the upright reproductive axes of *Sphacella subtilissima* Reinke (1891), do not form superior and

inferior secondary segments common to other members of this order. The appearance of the reproductive axes of *Battersia* is mostly filamentous, but the reproductive organs and their mode of development are similar to the development of these structures in other North Atlantic sphacelarioids. Only the persistent crustose condition of the vegetative plant and the lack of secondary segments in the upright axes set this species apart from other members of the order.

The possibility that *Battersia mirabilis* might be a reduced stage of another sphacelarioid, as suggested earlier by Sauvageau (1900), is not supported by our observations. From the many crusts we have studied, both vegetative and reproductive, there is no indication of a life history association with another member of the *Sphacelariales.*

The single representative of European *Battersia* we have seen is slightly more robust than the largest of our Massachusetts plants. Both crust size and the unilocular sporangia of the European plant average a few microns larger in length and width. The most conspicuous difference in the appearance of the European plant and those from the Massachusetts coast is the high degree of branching in many of the reproductive axes borne on the European plant (Figure II; see also Batters, 1889, *pl. X,* figures 2, 3–3a). Branching in the upright axes of the North American plants is relatively rare and, as yet, we have not seen the "clustered" appearance of sporangia as seen in Figure II, and illustrated previously by Batters (1889) and Reinke (1890). It is likely that the degree of branching is a function of plant age or, if consistently different between the American and European populations, it may have a genetic significance with the result that plants of the two disjunct populations now show morphological divergence.

Battersia mirabilis is yet another northern European species recognized from northeastern North America. The list of such species continues to grow, and the similarities between the two floras are increasingly apparent. A common origin for the two floras appears probable and understandable in the light of current geological concepts and floristic similarities. It is conceivable that several of the northern European species were accidently brought to our coast through human activities. Because these introductions have all occurred relatively recently, they appear to explain the relatively local presence of a handful of species from the total

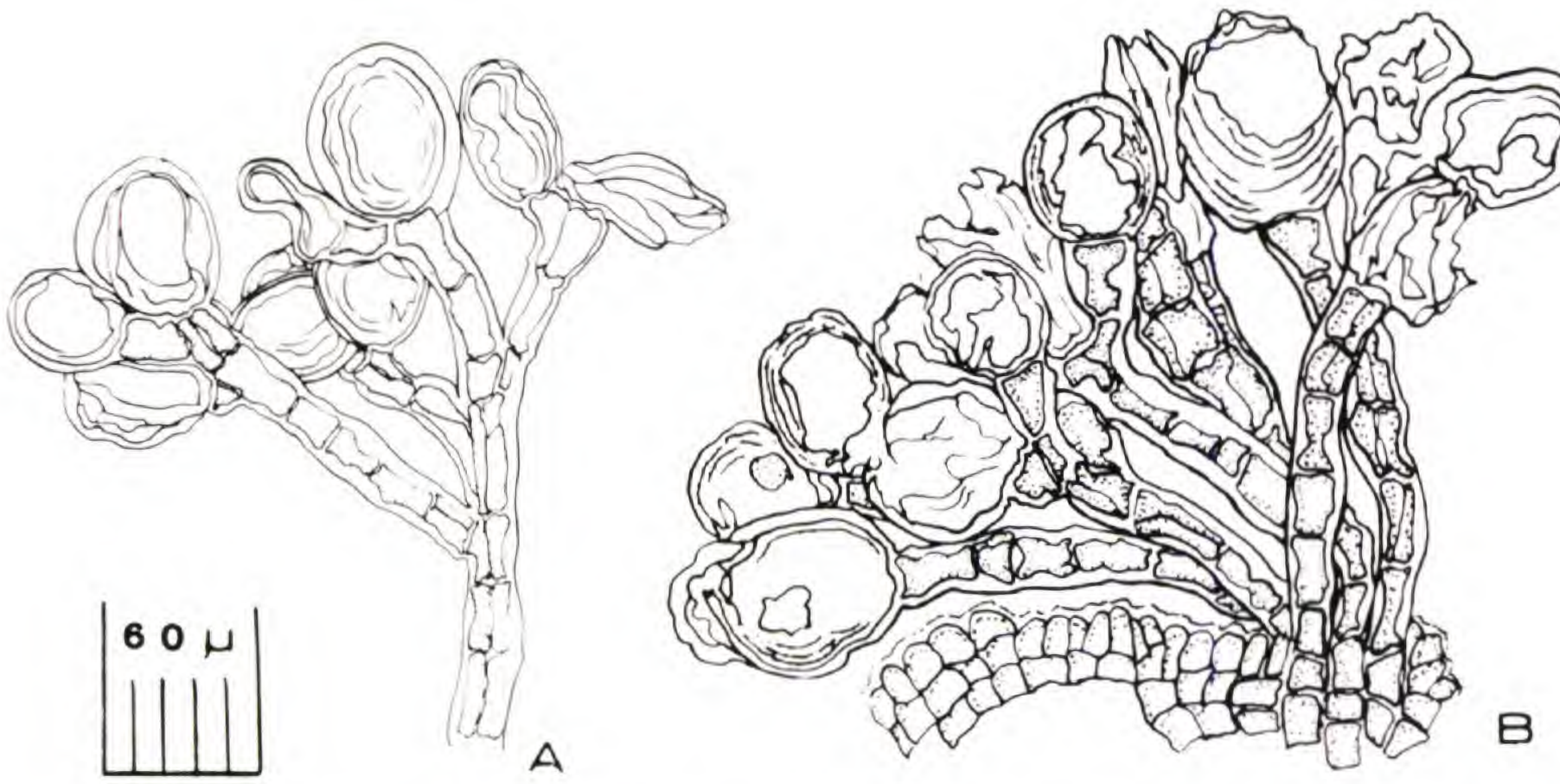

Figure II. Details of the unilocular sporangia and supporting axes of *Battersia mirabilis* collected from the type locality, Berwick-on-Tweed, Scotland, 1889, *leg. E. Batters*.

flora of northeastern North America. It is far more difficult to subscribe to the theory of accidental migration of the greater bulk of the northern European flora to our shores. A single floristic origin, implying considerable antiquity and necessitating extreme genetic conservatism, is the acceptable alternative.

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DEPARTMENT OF BOTANY
UNIVERSITY OF MASSACHUSETTS
AMHERST
MASSACHUSETTS 01002

A NEW STATION FOR COLEOCHAETACEAE IN MAINE

L. C. COLT, JR.

While collecting desmids in Knox County, Maine, I found four representatives of Coleochaetaceae previously unreported for the state, and another species that had been reported only once previously for Maine.

The collection site is in the extreme northwest corner of Crawford Pond. Covering approximately 580 acres, this pond is located in the town of Union and is three and one-half kilometers southeast of the junction of state routes 17 and 235. Immediately to the north of Crawford Pond, and contributing drainage and vegetative debris to the water body, lies a geological prominence known locally as Mars Hill.

All sampling was done during the month of July. Portions of vascular plant culms were collected by hand in water 5 centimeters deep or less, and within one meter of the shoreline. Dominant vascular plants of the collecting area include both floating (*Utricularia, Nymphaea* spp.) and emergent (*Typha, Juncus, Pontederia,* and *Sparganium* spp.) plants in such numbers as to effectively reduce water movement to negligible values.

With the seasonal contribution from the aquatic plants, and the detritus from the adjoining terrestrial ecosystem, the station has a mud substrate in excess of 4 centimeters at the outside limit of the station. Such shallow-water, vegetation-rich areas have been previously reported by this author (Colt & Hellquist, 1974) as providing the most suitable environment for the growth of abundant desmid populations. Apparently, judging by the coverage (60–80% of examined culm surfaces) of suitable substrates by the various Coleochaetaceae, such environments also are eminently appropriate for their rich growth.

Various culms (e.g., *Typha*) provided excellent sampling surfaces. All samples were preserved in Transeau's Solution immediately upon collection. This preservative (Prescott, 1972) has proven to be the most useful field preservative for the tychoplankter algae, as well as the epiphytes.

Harvey (1892) published the only previous record of Coleochaetaceae for Maine, that of *Coleochaete soluta* (Breb.) Pringsheim for Penobscot County, an area to the north of, and not contiguous to, the present location.

Determination was accomplished by means of the descriptions of Collins (1909), Smith (1950), and Prescott (1962). All samples have been retained in the author's personal collection until the desmid studies are completed. At that time representative samples will be placed in the Boston State College Herbarium. All figures were drawn from camera lucida studies made during determination.

Coleochaete irregularis Pringsheim (Figure 2).

This species occurred infrequently scattered on the culms. I was unable to find any instance of lateral joining, a phenomenon Prescott (1962) indicates to be of rare occurrence. The cells of my specimens were most often near-quadrate in shape and of irregular size. The size and growth of the thallus is in part due to the considerable number of diatoms scattered irregularly over the substrate surface. The thallus filaments were found growing between and around the diatoms indicating a growth period seasonally successive to the diatoms. A new record for Maine.

Coleochaete orbicularis Pringsheim (Not figured).

The reader is referred to Prescott, 1962, *pl. 18,* figures 3–5. This was the only member of the genus present with laterally attached filaments in a monostromatic disk. Thallus growth of this species seems to precede that of the diatoms. Common on *Typha* culms. A new record for Maine.

Coleochaete soluta (Breb.) Pringsheim (Figure 1).

The cells of the thalli from Crawford Pond fit the description of Collins (1909) more closely than that of Prescott (1962). Collins reports a different range of cell diameters (12–25 μm.) than does Prescott (17–25 μm.), and the diameters of the new collection range from 10–16 μm.

One reason for the variety of cell measurements is the tendency for the thallus to grow opportunistically. Reference to Figure 1, those cells labeled *b,* will show that cell division and subsequent cell growth proceeds wherever free substrate surfaces occur. When there are cells of that thallus present already, subsequent cells will tend to be much smaller (Figure 1, cells marked *a*). When some other structure, a diatom for example, is the obstacle, cell growth stops or proceeds in another direction (Figure 1, cells marked *c*). In the latter instance, the obstacle was a cell of *Tabellaria.*

Coleochaete soluta is fairly common on the *Typha* culms. This is the second report from Maine for this species.

Coleochaete pulvinata A. Braun var. **minor** L. C. Colt, var. nov. (Figures 3, 4, 5).

Frons pulvinata, filis ramosis et e centro communi radiantibus; cellulae filorum basalium a quadratis ad subhexagonales variantes, 7–18 μm. diametro; cellulae filorum radiantium 10–14 μm. diametro et 2–3 diameteri longae; oögonia globosa, rarenter subglobosa, corticata, 90–110 μm. diametro.

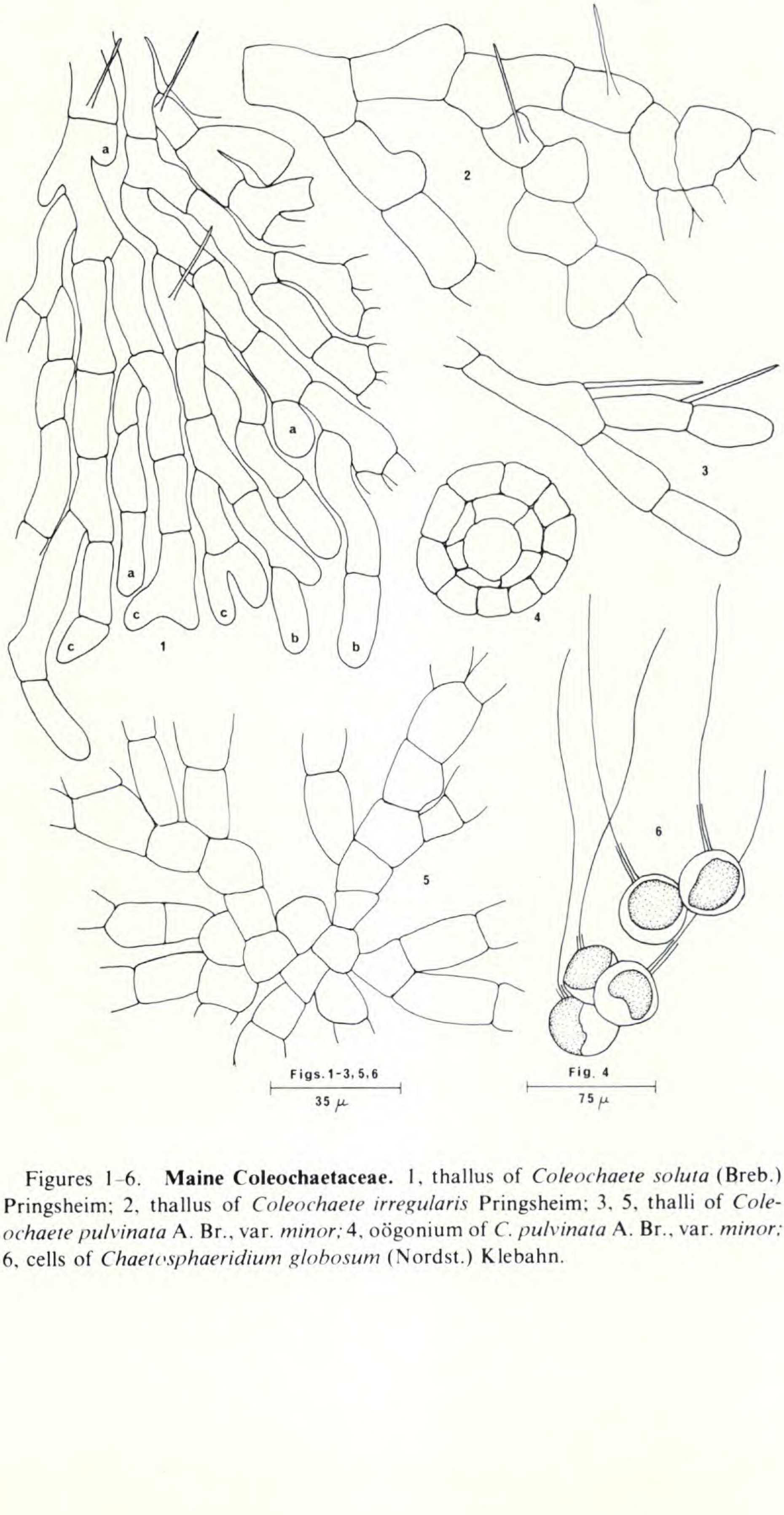
Frond pulvinate, composed of filaments radiating from a common center; cells of basal filaments quadrate to subhexagonal, 7–18 microns in diameter; cells of radiating filaments 10–14 microns in diameter and 2–3 diameters in length; oögonia globose, rarely subglobose, corticated, 90–110 microns in diameter.

This smaller variety of *Coleochaete pulvinata* corresponds readily to the descriptions published by both Collins (1909) and Prescott (1962), except for the very much smaller sizes. Comparatively, the measurements are:

	Collins	Prescott	var. *minor*
Cell diameter:	20–40 μm.	25–40 μm.	10–14 μm.
Length:	1½–2 dia.	35–75 μm.	2–3 dia.
Oögonia:	corticated, globose, about 150μm. diameter including cortex.	corticated, globose, 135–150 μm. diameter including cortex.	corticated, globose, 90–110 μm. diameter including cortex.

The thalli exhibited the common center cluster of cells (Figure 5) and a nearly hemispherical pulvinate form. Other than the smaller size the oögonia do not differ from those described by either Collins (1909) or Prescott (1962). All the individuals collected were found on dead *Typha* culms.

The holotype, *Colt s.n.*, was collected on July 28, 1969, from water 5 centimeters deep in the most northerly section of Crawford Pond, in the town of Union, Knox County, Maine. The collecting station is one-half meter from shore, on a direct line due east of the mouth of Daniels Brook, the latter situated on the west shore of that part of the pond. The type specimen is to be deposited in the Herbarium at Boston State College when the desmid studies are complete. A new record for Maine.



Figs. 1-3, 5, 6
35 μ

Fig. 4
75 μ

Figures 1–6. **Maine Coleochaetaceae.** 1, thallus of *Coleochaete soluta* (Breb.) Pringsheim; 2, thallus of *Coleochaete irregularis* Pringsheim; 3, 5, thalli of *Coleochaete pulvinata* A. Br., var. *minor;* 4, oögonium of *C. pulvinata* A. Br., var. *minor;* 6, cells of *Chaetosphaeridium globosum* (Nordst.) Klebahn.

Chaetosphaeridium globosum (Nordst.) Klebahn. (Figure 6).

The cells of this species were present both as individuals and in clusters. Prescott (1962) reports a similar pattern of occurrence in Wisconsin waters. Some setae were not observed, possibly due to the effects of the preservative solution. A new record for Maine. Croasdale (1935) and Webber (1963) have reported the species for Massachusetts.

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DEPARTMENT OF BIOLOGY
BOSTON STATE COLLEGE
625 HUNTINGTON AVENUE
BOSTON, MASSACHUSETTS 02115

CATALPA SPECIOSA NATURALIZED IN WESTERN MASSACHUSETTS[1]

C. JOHN BURK AND SCOTT D. LAUERMANN

The hardy catalpa, *Catalpa speciosa* Warder, is native from southwestern Indiana and southern Illinois west to Missouri and south to western Tennessee and northeastern Arkansas (Little, 1953). Escaped from cultivation or naturalized through much of the southeastern and midwestern United States, in New England it has been described as rare, occurring on roadsides and in waste places. Seymour (1969) includes illustrations useful in distinguishing *C. speciosa* from *C. bignonioides* Walt., a rather similar species native to the southeastern United States and rarely adventive in New England.

In western Massachusetts we have found *Catalpa speciosa* increasingly common on highway and railroad embankments and along the banks of streams, particularly in the vicinities of bridges. We have observed one abandoned asparagus field near Amherst, Massachusetts, in which the dominant woody invaders were three to four year old specimens of *C. speciosa*. In all instances, the probable origin of the escaped trees can be traced to one or more older cultivated specimens nearby.

We have also investigated a population of *Catalpa speciosa* in a floodplain forest in Northampton, Massachusetts, where the trees, 56 in number, are almost certainly naturalized and reproducing. The sites on which these specimens occur are the east and west banks of a channel and a rebuilt road edge constructed during a diversion of the Mill River in 1939. They occur in association with *Populus deltoides, Ulmus rubra, Acer saccharinum,* and *Fraxinus pennsylvanica.* The tallest *C. speciosa* is about 40 feet (12.2 m.) in height; most of the naturalized specimens are somewhat below the canopy of the larger native species while several which overhang the bank of the river show particularly luxuriant growth. Lower strata contain *Onoclea sensibilis, Pilea fontana, Vitis* spp. and *Sambucus canadensis.*

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[1]The research on which this report is based was supported in part by the Office of Water Resources Research, Department of the Interior as authorized under the Water Resources Act of 1964, P. L. 88-379.

Table 1. **Diameter classes (cm.) of Catalpa speciosa population.**

	<3	3–13.5	14–24.5	25–35.5
east bank	7	7	5	1
west bank	7	10	6	
road edge	4	6	2	1
total	18	23	13	2
percent of population	32.1	41.1	23.2	3.6

Table 2. **Age distributions within diameter classes of representative specimens of Catalpa speciosa** (saplings excluded).

age in years	diameter class (cm.) 3–13.5	14–24.5	25–35.5
1–5	1		
6–10			
11–15	3	1	
16–20	2	2	
21–25	1	3	
26–30			1
31–35			1

Diameters of all specimens of *Catalpa speciosa* at four feet (1.2 m.) from the ground were measured and grouped in four size classes (Table 1); ages were determined for 15 trees within the larger classes by increment borings or, in the case of a few felled trees, by ring counts (Table 2). The oldest tree, an estimated 32 years of age, became established soon after the time of the diversion. This tree and the next oldest (28 years) were the only specimens that fruited during 1975. The remaining specimens are distributed among the three smaller size classes and range from seedlings to trees 25 years of age.

The site is subject to periodic flooding and was inundated at least twice during the autumn of 1975. The form of the smaller specimens is strongly affected by the floods, with growth stunted the first few years and then occurring rapidly after height greater than the normal flood level is attained. For example, one sapling examined in detail was 2.64 m. tall with a diameter at base of 6.5 cm. Although the age of the tree was an estimated seven to eight years, over 2 m. of the total height was attained in the last two years, .96 m. in 1975 and 1.14 m. in 1976. The older portions of the shoot were extensively branched with numerous dead stems.

We have observed several other introduced or recently invasive species spreading in aquatic or semi-aquatic habitats in this section of the state (Burk, Lauermann, & Mesrobian, 1976). *Catalpa speciosa* is the only arborescent member of this group.

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DEPARTMENT OF BIOLOGICAL SCIENCES
SMITH COLLEGE
NORTHAMPTON
MASSACHUSETTS

REVISIONS TO A FLORA OF ESSEX COUNTY, MASSACHUSETTS

JAMES P. POOLE

In reviewing a Flora of Essex County, Massachusetts by Stuart K. Harris (Rhodora 77: 534. 1975) attention was called to the presence of numerous errors and discrepancies, but it was suggested that indubitably these would have been remedied had the author lived to make a final check of his manuscript before it was submitted for publication. It is not customary for a reviewer to list an extensive corrigendum nor a revision of a section of a publication, but in this instance they are presented as a tribute to a scholarly taxonomist. It is an effort to remedy the errors and discrepancies as Stuart Harris would have done had he been allowed the opportunity. There may even be errors that he would have detected that have escaped the eyes of the reviewer. — J.P.P.

FLORA OF ESSEX COUNTY, MASSACHUSETTS — STUART K. HARRIS — CORRIGENDA

Preface:

Par. 1, line 2. *Read* second edition *for* fifth edition.
Par. 4, line 3. *Read* completely *for* completed.
line 6. *Read* End Map *for* End Maps.
Par. 5, line 2. *Read* Tiffney *for* Tiffeny.

Page vii:

Par. 1, line 10. *Read* Maple *for* Mapel.

Page 1:

Par. 3, line 6. *Should read* through which a channel has been dredged.
Par. 5, line 2. *Read* northeasterly *for* northwesterly.

Page 2:

Par. 6, line 1. Read *Betula populifolia* for *Betula lenta.*
Par. 7, line 6. *Read* indigenous *for* introduced.

Page 15, under SPECIES EXCLUSAE:

Read *Bouteloua* for *Bouteloa.* Also, *B. gracilis* is listed in the Catalog (p. 74).
Setaria verticillata is included in the Catalog (p. 80).
Dipsacus sylvestris (p. 19) is included in the Catalog (p. 229).

Pages 20–23:

If the figures listed in the STATISTICAL SUMMARY are checked with the Catalog, occasional disagreement is evident. The fig-

ure (1767) for GRAND TOTAL TAXA does not include the totals for varieties, forms, and hybrids.

Page 24:

Read The Fig as a Hardy Plant *in third item.*

Read 1905 *for* 1907 *in last item.*

Page 25:

First item should be ascribed to manuscript notes of Wm. Oakes.

First Mary A. Day reference (1899), *read* Rhodora **1:** 111, 138, 158, 174, 194, 208 *for* Rhodora **1:** 174–176.

The following reference (1900), *read* Rhodora **2:** 73 *for* Rhodora **2:** 74.

Page 28:

Second reference for C. N. S. Horner, *read* 1883 *for* 1885.

Page 32:

Last two references for J. L. Russell, *read* Am. Nat. **3:** *for* Am. Nat. **2:**.

Page 34:

L. C. Wheeler reference, *read* 1941 *for* 1940.

K. M. Wiegand reference, *read* 1912 *for* 1911.

Page 35:

Par. 4, line 1. *Read conscientiously for* conscientiously.

Par. 5, line 4. *Read* to be thrust *for* to be a thrust.

Page 38:

Fifteenth reference, *read* Rhodora **43:** *for* Rhodora **3:**.

All Appalachia references are New Series.

All Appalachia volume **9** references should be dated 1943.

An additional Harris publication, Notes on Solidago, Section *Euthamia,* Rhodora **45:** 413. 1943, should precede the last entry.

Page 39:

Twelfth item, *read* Appalachia **20:** *for* Appalachia **17:**.

Page 40:

For Arthur S. Pease reference *read* Flora of Northern New Hampshire.

For volume numbers of the Bean, Hill, and Harris references *read* **65:** *for* **63:** *and* **69:** *for* **67:**.

Page 51:

Read *Woodwardia virginica* for *Woodwardia Virginica.*

Page 54:

After *J. horizontalis, read* Moench *for* moench.

Page 55:

After *S. fluctuans, read* Morong *for* morong.

Page 60:
After *B. mollis,* read *leiostachys* for *leiostychys.*
Page 65:
Read TRIPLASIS *for* TRIPSALIS.
Page 67:
Under LOLIUM, read *L. temulentum* for *L. temulatum.*
Page 74:
Under SPARTINA, read *S. patens* var. *monogyna* for *S. patens* var. *morogyna.*
Page 80:
Under *Setaria verticillata read* Raynal *for* Raymond.
Page 87:
Under CAREX, read *C. foenea* for *foena.*
Page 93:
Under *Carex swanii, read* Charles Walter Swan *for* Charles Water Swan.
Page 99:
Under JUNCUS, read *J. effusus* var. *pylaei* for var. *dylaei.*
Page 108:
Under EPIPACTIS, *insert* Crantz *after E. helleborine* (L.).
Page 121:
Fourth variety of *P. amphibium,* insert f. *hirtuosum* before (Farw.).
Page 123:
Read *P. convolvulus* for *gonvolvulus.*
Page 146:
Read *R. islandica* var. *fernaldiana* for *Fernaldiana.*
Page 156:
Under *G. canadense* var. *camporum, insert* & Weatherby *after* Fern.
Page 163:
L. tomentosum L., introduced from Mediterranean region.
Page 168:
Under STROPHOSTYLES, read *S. helvola* for *helvoela.*
Page 171:
Under XANTHOXYLUM, read *X. clava-herculis* for *hercules.*
Page 172:
Read EUPHORBIACEAE (Spurge Family) *for* EUPHORBIA (Spurge Family).
Page 186:
Read CUPHEA R. Br. *for* P. Br.

Page 202:
Read GENTIANACEAE *for* GENTIANACEA.
Read SABATIA Adans. Sabatia *for* Sabatia Adans. Sabatia.
Page 204:
Under IPOMEA, read *I. coccinea* for *coceinea.*
Page 205:
Under *C. gronovii,* last line of data, *read* Morong *for* Norong.
Page 206:
Under LITHOSPERMUM, *read L. arvense* Corn Gromwell *for* Cromwell.
Page 214:
Solanum melogena var. *esculentum,* introduced from India.
Page 221:
Under BIGNONIACEAE, *read* CAMPSIS *for* GAMPSIS.
Page 235:
Line 1, *read* × *S. asperula for* × *s. asperula.*
Page 241:
Read HELICHRYSUM *for* ELICHRYSUM, nomen conservandum (Int. Code).
Index
Page 262:
Under Carex, *read* foenea *for* foena; *read* seorsa *for* sorsa *and insert after* scoparia.
Under Chickweed, *read* wintergreen *for* Wintergreen.
Page 263:
Insert Corn-Cockle p. 132 *after* Cornaceae.
Delete Elichrysum.
Under Eupatorium *read* 232 *for* 231.
Page 264:
Read Galium *for* Gallium.
After "Common" under Hairgrass, move rest of column three spaces left.
Page 265:
After Helianthus, *insert* Helichrysum p. 241.
Page 266:
Delete Medic p. 153.
Read Megalodonta *for* Megalondonta.
Page 267:
Read Sambucus *for* Sambuccus.
Page 269:
Read Wild-oats *for* Wild-Oats.
Read Zannichellia *for* Zanichellia.

STATISTICAL SUMMARY

	Genera		Species		Varieties		Forms and Hybrids	
DIVISION PTERIDOPHYTA	Nat.	Int.	Nat.	Int.	Nat.	Int.	Nat.	Int.
Fam. Equisetaceae	1		5		1		12	
Lycopodiaceae	1		7		4			
Selaginellaceae	1		2					
Isoëtaceae	1		4					
Ophioglossaceae	2		7		1		4	
Osmundaceae	1		3		1		3	
Schizaeaceae	1		1					
Polypodiaceae	13		25		7		12	
Marsileaceae	1		1					
DIVISION SPERMATOPHYTA								
SUBDIVISION GYMNOSPERMEAE								
Fam. Taxaceae	1		1					
Pinaceae	7		11	3	1			
SUBDIVISION ANGIOSPERMAE								
CLASS MONOCOTYLEDONEAE								
Fam. Typhaceae	1		2				1	
Sparganiaceae	1		8					
Zosteraceae	4		23		8		2	
Najadaceae	1		2					
Juncaginaceae	2		2					
Alismataceae	3		8		1		3	
Hydrocharitaceae	2		3					
Gramineae	40	20	119	60	27	7	13	13
Cyperaceae	11		154	4	14		10	
Araceae	5		6				6	
Lemnaceae	3		4					
Xyridaceae	1		3					
Eriocaulaceae	1		2					
Commelinaceae		2		2				
Pontederiaceae	2		2				3	
Juncaceae	2		18		7		3	
Liliaceae	13	7	21	13	2	1	2	
Amaryllidaceae	1	1	1	1				
Iridaceae	2		6	3				
Orchidaceae	12	1	28	1	3		1	

CLASS DICOTYLEDONEAE	Genera Nat.	Genera Int.	Species Nat.	Species Int.	Varieties Nat.	Varieties Int.	Forms and Hybrids Nat.	Forms and Hybrids Int.
SUBCLASS ARCHICHLAMYDEAE								
Fam. Salicaceae	2		14	8	3	1	5	
Myricaceae	2		3		1			
Juglandaceae	2		7					
Corylaceae	5		11		3		4	
Fagaceae	3		10	3		1		
Ulmaceae	2		3	1			4	
Moraceae		3		4				
Cannabinaceae		2		3				
Urticaceae	5		5	2	1			
Santalaceae	1		1					
Loranthaceae	1		1					
Aristolochiaceae	1		1					
Polygonaceae	3	1	26	16	6	3	4	
Chenopodiaceae	5	4	17	12	3	3		
Amaranthaceae	2		5	4				
Nyctaginaceae	1			2				
Phytolaccaceae	1		1					
Aizoaceae		2		2				
Portulacaceae		2		3				
Caryophyllaceae	7	8	15	26	1		1	
Ceratophyllaceae	1		2					
Nymphaeaceae	3	2	3	2	1		1	
Ranunculaceae	10	3	27	9	6	1	4	1
Lardizabalaceae		1		1				
Berberidaceae	2		1	2				
Magnoliaceae	1	1	1	2				
Lauraceae	2		2					
Papaveraceae	3	4	3	6				
Capparidaceae	2		1	2				
Cruciferae	7	20	13	39	2	2		2
Resedaceae		1		2				
Sarraceniaceae	1		1					
Droseraceae	1		2					
Crassulaceae	1	2	1	6				
Saxifragaceae	7	2	11	6			1	
Hamamelidaceae	1		1		1			
Platanaceae	1		1					
Rosaceae	14	5	63	28	8	1	4	1

CLASS DICOTYLEDONEAE	Genera Nat.	Genera Int.	Species Nat.	Species Int.	Varieties Nat.	Varieties Int.	Forms and Hybrids Nat.	Forms and Hybrids Int.
SUBCLASS ARCHICHLAMYDEAE								
Fam. Leguminoseae	12	16	28	41	4	4		3
Linaceae	1		2	1				
Oxalidaceae	1		4	2				3
Tropaeolaceae		1		1				
Geraniaceae	1	1	3	6				
Rutaceae		4		5				
Simaroubaceae		1		1				
Polygalaceae	1		5		2			
Euphorbiaceae	2	1	6	5				
Callitrichaceae	1		3	1				
Anacardiaceae	1	1	5	1	2			
Aquifoliaceae	2		5		1		1	
Celastraceae	1	1	1	2				
Aceraceae	1		5	4	1			
Hippocastanaceae		1		1				
Balsaminaceae	1		1	1				
Rhamnaceae	1	1	2	2				
Vitaceae	2		6	1			1	
Tiliaceae	1		2	1				
Malvaceae	1	4	1	9				1
Guttiferae	1		9	2	1		1	
Elatinaceae	1		2					
Cistaceae	3		9		1			
Violaceae	1		18	2	1		3	
Thymelaeaceae	1	1	1	1		1		
Lythraceae	3	1	3	2	1	1		
Nyssaceae	1		1					
Melastomataceae	1		1					
Onagraceae	4	1	15	4	1			
Haloragaceae	2		6				2	
Araliaceae	2		4					
Umbelliferae	12	11	16	11			1	
Cornaceae	1		8					
SUBCLASS METACHLAMYDEAE								
Fam. Clethraceae	1		1					
Pyrolaceae	4		9		1			
Ericaceae	12	1	24	1	2		5	

SUBCLASS METACHLAMYDEAE	Genera Nat.	Genera Int.	Species Nat.	Species Int.	Varieties Nat.	Varieties Int.	Forms and Hybrids Nat.	Forms and Hybrids Int.
Fam. Diapensiaceae		1		1				
Primulaceae	5	3	9	6	1		1	1
Plumbaginaceae	1		2					
Oleaceae	1	2	3	3	2			
Gentianaceae	4	2	6	3			2	
Apocynaceae	1	1	3	2				
Asclepiadaceae	1	1	8	1				
Convolvulaceae	2	1	3	5			2	1
Polemoniaceae		2		2				
Boraginaceae	2	8	3	13				
Verbenaceae	1		2	3				
Labiatae	10	18	20	31	5	2	4	
Solanaceae	2	7	3	22		1		
Scrophulariaceae	13	6	26	22	4		5	2
Bignoniaceae		2		2				
Martyniaceae		1		2				
Pedaliaceae		1		1				
Orobanchaceae	2		2					
Lentibulariaceae	1		8					
Phrymaceae	1		1					
Plantaginaceae	1		3	4	1	1		1
Rubiaceae	4	2	15	8			2	
Caprifoliaceae	6	2	13	7			1	
Valerianaceae		1		1				
Dipsacaceae	1	3	1	3				
Cucurbitaceae	2	3	2	5		1		
Campanulaceae	3	1	8	3				
Compositae	24	36	130	88	29	6	27	7
Totals	Native 1543		Adventive 697					
							GRAND TOTAL TAXA	2240

SUMMARY BY MINOR GROUPS

	Native	Introduced	Total
Families	116	17	133
Genera	405	245	650
Species	1209	624	1833
Additional Varieties	173	37	210
Additional forms and hybrids	161	36	197

DARTMOUTH COLLEGE
HANOVER, NEW HAMPSHIRE 03755

NOTABLE PLANTS OF RATTLESNAKE MOUNTAIN, PORTER, MAINE

Rattlesnake Mountain (1179 feet) lies two and a half miles north of Porter Village, in southern Oxford County, and two miles east of the New Hampshire border. The mountain is aptly named, for in a history of that town written by Moulton in 1879 he states that in the spring of 1820, eleven rattlesnakes were killed in about one hour. Moulton then adds that the reptile is apparently now extinct in the town since none has been seen for many years.

On June 8, 1974, C. Paul Wight of Old Orchard Beach and I visited this mountain as we had been impressed by some prominent ledges on its southern side, which we observed from a road. The southern slope of Rattlesnake Mountain is mostly a well developed hardwood forest; some stone walls, leading partly up the mountain, indicate earlier fields and pastures. On the moist ledges above the wooded slope we discovered *Ranunculus fascicularis* Muhl. growing abundantly. This locale sets a new range limit for this species. The farthest north it had been recorded prior to this discovery was at Nottingham, New Hampshire, where Dr. Albion Hodgdon observed the species. On the higher ledges *Arabis missouriensis* Greene grew sparingly.

Subsequent trips were made independently by Christopher Campbell. He and I also visited the site together. On one such trip in the summer of 1974 he discovered *Vitis aestivalis* var. *argentifolia* (Munson) Fern., which was a new record for the state.

Other plants found were: *Selaginella rupestris* (L.) Spring, *Woodsia obtusa* (Spreng.) Torr., *Asplenium Trichomanes* L., *Hystrix patula* Moench, *Oryzopsis racemosa* (Muhl.) Fern., *Silene Antirrhina* f. *Deaneana* Fern., *Hepatica americana* (DC.) Ker, *Cerastium arvense* L., *Ceanothus americanus* L., *Geranium Bicknellii* Britt., *G. carolinianum* L., *G. Robertianum* L., *Epilobium ciliatum* Raf., *Specularia perfoliata* (L.) DC., *Gerardia flava* L., and *Antennaria plantiginifolia* (L.) Hook.

Specimens have been deposited at the herbarium of the University of Maine.

L. M. EASTMAN
OLD ORCHARD BEACH
MAINE 04064

NOTICE OF PUBLICATION

L. D. Howard. *Moss Flora of New England, New York and Southeastern Canada.* [vi +] 74 pp. Hardbound. Burlington, Vermont. 1975. — A moss flora covering the geographical area outlined in the title, and adapted from A. J. Grout's *Moss Flora of North America,* has recently been published by the University of Vermont. Including keys to genera and species and notes on species habitats, this volume should prove of value to northeastern botanists, both amateur and professional, interested in our moss flora.

Copies, at $4.25 each (plus 50¢ postage) can be purchased from: University Store, On The Campus, University of Vermont, Burlington, VT 05401.

Vol. 79, No. 817, including pages 1–167, was issued March 18, 1977.

INDEX to

Volumes 51–75, (1949–1973)

of RHODORA

The publication of this new index to volumes 51–75 of **RHODORA** provides a supplement to the index to the first 50 volumes (1899–1948). It provides botanists access to a large body of systematic and floristic research, so basic to botanical work in New England and North America, published in the pages of **RHODORA** from 1949 to 1973.

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RHODORA **April, 1977** **Vol. 79, No. 818**

CONTENTS

Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

Vol. 79 July, 1977 No. 819

The New England Botanical Club, Inc.

Botanical Museum, Oxford Street, Cambridge, Massachusetts 02138

Conducted and published for the Club, by
ROLLA M. TRYON, Editor-in-Chief

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Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 79 July, 1977 No. 819

A REVISION OF THE GENUS GALINSOGA (COMPOSITAE: HELIANTHEAE)

JUDITH M. CANNE

Most amateur and professional botanists are familiar with the genus *Galinsoga* through acquaintance with *G. parviflora* Cav. and *G. quadriradiata* Ruiz and Pavon (*G. ciliata* (Raf.) S. F. Blake). Both species typically occupy areas disturbed by man (i.e., they are weedy in the sense of Baker, 1966, p. 147) in the New World and Europe, and also have been introduced into Asia, Africa, Australia, and other temperate and subtropical regions of the world. Although the genus has attracted the attention of numerous European botanists (e.g., Müller, 1914; Brenan, 1939; Giacomini, 1947, 1950; Lousley, 1950; Haskell & Marks, 1952, 1954) and several American botanists (e.g., Robinson, 1894, 1899; Turner, 1965, 1966; Shontz & Shontz, 1970; Braden & Cialone, 1971; Ivany & Sweet, 1973) it has never been studied in a comprehensive taxonomic manner.

Thellung (1916) prepared a treatment of only the European species of *Galinsoga,* while St. John and White (1920) provided a synoptic key to the species occurring primarily in the United States. These studies have dealt principally with species of *Galinsoga* from areas in which the species are non-indigenous. The genus apparently is native to Mexico, and in this region the greatest diversity and taxonomic complexity are found.

Recognition of taxonomic limits within *Galinsoga,* particularly at the specific level, has been difficult (DeCandolle, 1836; Robinson, 1894; St. John & White, 1920; Lousley, 1950; Turner & King, 1964). One cause of this difficulty has been that many of the morphological character states used to distinguish the taxa have proven to be variable and intergrading. In most instances, the use by earlier workers of ray corolla color, presence or absence of pappus, and pubescence

of the achenes has proven to be unreliable as a means of distinguishing species. The recognition of new species, varieties, and forms on the basis of these inconstant characters has resulted chiefly from a lack of understanding of populational character variation. The primary objective of this investigation has been to clarify the specific limits in *Galinsoga* by assessing the morphological variation at the intra- and interpopulational levels. Cytological, distributional, and ecological data have been used as well.

Perhaps an even more puzzling problem than the specific relationships in *Galinsoga* has been the confusion regarding generic limits. DeCandolle (1836) questioned the placement of five of the six species he treated as comprising the genus. Bentham and Hooker (1873) commented on the difficulty of distinguishing *Galinsoga* and *Vargasia* DC., and Robinson (1894) noted the difficulties in differentiating *Galinsoga* from several closely allied genera. Blake (1915) established the genus *Stenocarpha* to accommodate a species of *Galinsoga,* and Turner (1966) submerged the genus *Stemmatella* into *Galinsoga.* In addition, the generic delimitation of *Galinsoga* has remained a point of taxonomic confusion even though the genera in the subtribe Galinsoginae most closely related to *Galinsoga* (i.e. *Tridax* L., *Stenocarpha* S. F. Blake, *Sabazia* Cass., *Selloa* HBK., *Tricarpha* Longpre, and *Cymophora* Robins.) have been the subjects of recent taxonomic revisions (Powell, 1965; Turner, 1965; Longpre, 1970; Turner & Powell, 1977). The discussion and resolution of these generic problems associated with *Galinsoga* are reported separately (Canne, in press) and not restated here. The generic circumscription adopted therein, however, is used in this revision.

In the present treatment, *Galinsoga* is recognized to include fourteen species in three sections. From this viewpoint the genus is seen as a Mexican, Central American, and South American taxon of subtropical and temperate regions with the greatest concentration of species in central Mexico. The most significant departure from previous treatments is the enlargement of the generic limits of *Galinsoga* to include *Stenocarpha* and one species each of *Sabazia* and *Tricarpha.* The resultant assemblage of taxa represents a more useful perspective on interspecific relationships as well as providing a better understanding of affinities with other genera in the subtribe Galinsoginae.

TAXONOMIC HISTORY

The first description of *Galinsoga* appeared in the second volume of L. E. Feuillée's *Journal des Observations Physiques, Mathematiques et Botaniques* (1714). Feuillée applied the polynomial "Bidens Mercurialis folio, flore radiato" to the plant he described, and provided an excellent illustration of the taxon later to be known as *Galinsoga parviflora* Cav.

The first valid description of *Galinsoga* appeared in 1794 in Ruiz and Pavon's *Florae Peruvianae et Chilensis Prodromus.* An illustration of various features of the capitulum was provided, but no specific epithet was assigned to the taxon described. The genus was named in honor of Dr. D. Mariano Martínez de Galinsoga, a Spanish physician and director of the Botanical Garden at Madrid. Cavanilles, in his *Icones et Descriptiones Plantarum* of 1795, described the lectotype species, *Galinsoga parviflora,* which he noted was grown in Paris as early as 1785 from seed sent from Peru by Mr. D. Dombey who had traveled with Ruiz and Pavon in Peru and Chile. At the same time, Cavanilles described *G. trilobata,* a species later transferred to *Tridax* by Hemsley (1881).

Ruiz and Pavon published two new names in *Galinsoga, G. quinqueradiata* and *G. quadriradiata,* in the *Systema Vegetabilium Florae Peruvianae et Chilensis* of 1798. Apparently annoyed by Cavanilles' earlier publication of *G. parviflora,* they redescribed his species as their *G. quinqueradiata* and relegated *G. parviflora* Cav. to synonymy.

Roth (1800) published the generic name *Wiborgia,* including one species, *W. acmella,* which he later (1806) realized was synonymous with *Galinsoga parviflora* Cav. The Roth name has since been rejected (*International Code of Botanical Nomenclature,* Appendix III, no. 3661, Stafleu, *et al.,* 1972) in favor of *Wiborgia* Thunberg (1800), a conserved name for a genus in the Leguminosae. In 1808 Poiret formed *Vigolina* as a substitute name for Roth's genus.

Recognizing the generic differences between *Galinsoga parviflora* Cav. and *G. trilobata* Cav., Humboldt, Bonpland and Kunth (1818) included *G. parviflora* in Roth's *Wiborgia* (placing *W. acmella* in synonymy) and described *W. urticaefolia* as new. Meanwhile, they included *G. trilobata* in their genus *Galinsogea* with

the newly described *G. balbisioides*. *Galinsogea* HBK. is now recognized as synonymous with *Tridax* L. (Powell, 1965).

Only three additional *Galinsoga* names appeared following the publication of the two species by Ruiz and Pavon (1798) until Sprengel (1820) named *G. angustifolia* and later in 1826 included four new combinations and four newly described species in the genus. One additional name, *G. resinosa* Hook. & Arn. (1830), appeared before DeCandolle treated the genus in 1836. DeCandolle questioned the placement of five of the six species he included in the genus and referred seven additional species to five other genera. DeCandolle also described as new the genus *Vargasia* and included one species, *V. caracasana*. *Vargasia* DC. is a later homonym of *Vargasia* Bertero ex Spreng. (1825), and *V. caracasana* was transferred to *Galinsoga* by Schultz-Bipontinus (1866).

Rafinesque (1836) described the genus, *Adventina*, in which he included two species. Blake (1922) recognized Rafinesque's taxa, which were described in detail, as synonymous with previously described species of *Galinsoga*.

Six additional names were published in *Galinsoga* in the period between 1836 and the appearance of Bentham and Hooker's *Genera Plantarum* in 1873. In this work, Bentham furnished the first description for the genus *Stemmatella*. The name *Stemmatella congesta* Wedd. had appeared in a list of plants published by Schultz-Bipontinus (1865) and the name remained a *nomen nudum* until Hoffmann (1890) provided a description. Hieronymus (1901) named three other species of *Stemmatella*, one of these being a transfer of *Wiborgia urticaefolia* HBK. This species of *Wiborgia* earlier had been referred to the genus *Jaegeria* by Sprengel (1826), to *Sabazia* by DeCandolle (1836), to *Baziasa* by Steudel (1840), and to *Galinsoga* by Bentham (1852). All species of *Stemmatella*, except *S. lehmannii* Hieron., were referred to *Galinsoga* by Turner (1966).

Additional species of *Galinsoga* were described by Grisebach (1879), Hemsley (1879), Rusby (1893), and Hieronymus (1901, 1907). In 1915, S. F. Blake proposed the genus *Stenocarpha* to accommodate *Galinsoga filiformis* Hemsl.

Thellung (1916) discussed at length the two species of *Galinsoga* known to occur in Europe and described several varieties and forms in *G. parviflora* and *G. quadriradiata*. Apparently unaware of Thellung's work, St. John and White (1920) acknowledged none of the names proposed by him when they treated the *Galinsoga*

species occurring in the United States. In their study, St. John and White also described as new *G. bicolorata* from Mexico, *G. purpurea* from Bolivia, and raised to specific rank *G. parviflora* var. *semicalva* A. Gray as *G. semicalva.* Since the treatment of St. John and White, three additional species of *Galinsoga* have been newly described (Cuatrecasas, 1954; Cronquist, 1965; McVaugh, 1972).

DISTRIBUTION AND ORIGIN

Galinsoga parviflora and *G. quadriradiata* are the most wide ranging species of *Galinsoga. Galinsoga parviflora* is weedy in temperate regions of the world and *G. quadriradiata* has a near continuous distribution from southern Canada to Argentina and is known from the Old World as well. The next most widely distributed species is *G. mandonii* which is confined to the Andean regions of Peru, Bolivia, and northern Argentina. Among the remaining species, nine are known only from restricted mountainous areas of western and central Mexico. *Galinsoga caligensis* is known only from the coastal deserts of Peru, and *G. boliviensis* has been reported from the La Paz region of northern Bolivia.

This pattern of distribution strongly suggests that *Galinsoga* originated in the mountainous areas of west-central Mexico. Two of the four species in South America are the weedy *G. parviflora* and *G. quadriradiata.* Their spread into the United States and the Old World within the last 150 years is well documented (see below). Their apparent migration southward is less well known but presumably was aided significantly by the advent of agriculture and road building. One of the other species in South America, *G. boliviensis,* appears to be derived from *G. quadriradiata,* and the extreme desert habitat occupied by *G. caligensis* would indicate that this species is the product of intense selection in a limited habitat. Supporting evidence for a Mexican origin of the genus is the fact that the four genera most closely related to *Galinsoga,* i.e. *Tridax, Cymophora, Sabazia,* and *Selloa,* are also centered in central Mexico (Powell, 1965: Turner & Powell, 1977; Longpre, 1970).

The migration and spread of *Galinsoga quadriradiata* into the United States and Canada during the last century has been traced by Shontz and Shontz (1970) using herbarium material and published reports of sightings. While the data of these authors were

compiled only recently, this type of study has occurred in Europe since the end of the 19th century for both *G. quadriradiata* and *G. parviflora*. Accounts of new sightings appeared regularly from the British Isles in the *Botanical Society and Exchange Club of the British Isles*, from France in *Bulletin de la Société Botanique de France* and *Le Monde des Plantes*, and from Austria and nearby areas in *Osterreichische Botanische Zeitschrift*.

The rapidity with which the two species spread prompted many authors to collect this information into reviews in an attempt to document succinctly the migration of *Galinsoga* through the Old World. The works of Kronfeld (1889) are among the earliest of these compilations. Kronfeld dealt only with *G. parviflora*, the first *Galinsoga* to enter Europe, and he reviewed the nomenclatural history of the species as he knew it, noting that plants had been grown in the Botanic Gardens in Paris and Madrid as early as 1794. Included was a chronological listing of herbarium records and literary references for collections and sightings of *G. parviflora* in areas we know today as Italy, Switzerland, Austria, Hungary, Germany, and England. In 1892, Bargogli elaborated on the spread of *G. parviflora* in Italy, and Buchenau discussed the early history of *G. parviflora* and the nomenclatural confusion which seems to have developed about the species almost as soon as it was recognized on the continent.

Müller (1914) produced a lengthy treatise on *Galinsoga parviflora* including synonymy, common names in use at the time in Germany, morphology, diseases of the species, germination as influenced by achene depth in soil and temperature, and a long discussion of the distribution of the taxon in Europe. The text was accompanied by illustrations of seedlings, mature plants, and parts of the capitulum.

By the turn of the century, *Galinsoga quadriradiata* had entered Europe. Thellung (1916) provided a summary of localities for *G. quadriradiata* and *G. parviflora*, and then subdivided both taxa into numerous varieties and forms. Jovet (1928) and Jovet and Vergnet (1928) reported the introduction of *G. quadriradiata* in France and reviewed the spread of *G. parviflora* in that country.

The following year Majdecka-Zdziarska (1929) contributed a thorough discussion of European and Asian distributions for both Galinsogas as well as synonymy, morphology, gross anatomy, and germination data for *G. quadriradiata* (as *G. hispida* Benth.) and

G. parviflora. Subsequent papers by Jovet and Vergnet (1930), Magnel (1930), Wilczek (1930), Jovet (1931), Homeiu (1934), van Soest (1941), Giacomini (1947), Dizerbo and Nehou (1952), Haskell and Marks (1952, 1954), Lacey (1956), and others continued to follow the spread of *Galinsoga.* The primary emphasis was on European, and to a lesser extent, early Asian sightings.

Little seems to have been written concerning the entrance of *Galinsoga* into Africa, eastern Asia, and the Pacific regions. However, the representative specimens included in the taxonomic section of this paper document the presence of *G. parviflora* and *G. quadriradiata* in the New and Old Worlds. Data from herbarium specimens indicate that *G. parviflora* has become established in India, eastern Asia, the Pacific Islands, Africa, and Australia. *Galinsoga quadriradiata,* on the other hand, has been introduced into India, Nepal, Japan, the Philippines, and parts of Africa, but the smaller number of collections suggests that *G. quadriradiata* is less abundant in these areas than is *G. parviflora.*

The rapid spread of *Galinsoga parviflora* and *G. quadriradiata* is, of course, a reflection of their weediness. Allard (1965, p. 49) cited "*Galinsoga* species" in a list of taxa which ". . . on a world-wide basis [are] the most successful noncultivated colonizers . . ." Biological characteristics which predispose a species toward weediness have been mentioned by Baker (1965, pp. 166, 167). For the most part, both *G. parviflora* and *G. quadriradiata* show these features. They have no special requirements for germination, show rapid seedling development, flower after a short period of vegetative growth, produce flowers and fruits throughout the growing season, are self- and cross-fertile, produce large amounts of fruits in favorable conditions, and produce fruits in a wide range of environmental circumstances (see Ivany & Sweet, 1973, for one of the more recent discussions of many of these characteristics in both species and Shontz & Shontz, 1972, for a discussion of *G. quadriradiata*).

MORPHOLOGY

The determination of the constancy of morphological features forms the basis for assessing their reliability as taxonomic characters. Much of the confusion concerning specific limits in *Galinsoga* has developed because the variability of several morphological

features used as taxonomic characters has not been documented at the populational level or throughout the range of most species. *Galinsoga,* particularly the weedy species, is notable for the number of morphological attributes which vary at the inter- and intra-populational levels. This variability has probably been promoted by the self-compatibility of the plants, which has allowed the establishment of isolated inbreeding populations following achene dispersal. The most outstanding example of variability occurs in the *G. quadriradiata* complex which is treated here as one polymorphic species. Vegetatively the species is very plastic, and features of the capitulum also show a wide array of morphic types. The other weedy species, *G. parviflora* and *G. mandonii,* show to a lesser degree many of the same kinds of morphological variability expressed in *G. quadriradiata.*

In light of the variability of certain morphological features within the genus, the taxonomic value of vegetative and floral characters is discussed at some length below. Vesture terminology follows that of Lawrence (1951), whereas other terminology is used as in Stearn (1966). Measurements were made from dried herbarium specimens except for features of the head. When abundance of material permitted, heads were soaked in detergent solution and measurements made from the expanded structures.

Habit. All species of *Galinsoga* are herbaceous annuals with erect stems. *Galinsoga calingensis,* however, is also commonly decumbent.

Stems. Stems are striated throughout their length and are often reddish in color. Stem pubescence consists of multicellular, appressed to spreading trichomes of varying lengths and densities. Glandular capitate trichomes are interspersed on the uppermost branches in some species. This character is not always stable and, in most cases, cannot be used as a taxonomic feature. Branching is opposite, and most species vary from simple to multibranched.

Roots. All species have a slender taproot with multiple secondary roots. In weedy species the plants are often shallowly rooted and show poor development of the taproot but extensive growth of secondary roots and adventitious roots from the base of the stem.

Capitulescence. In all species the heads are arranged in terminal and axillary cymose clusters. The number and size of heads, and peduncle length are useful for recognition of sections.

Heads. Within certain limits, many features of the heads are useful

as taxonomic characters. Phyllaries — The number of series of phyllaries is stable within each species and is a useful character. The number, relative size, shape and pubescence of the outer and inner phyllaries are also reliable characters. Pales — The pales are dimorphic in most species of *Galinsoga.* The outermost pales are broader and usually longer than the inner. Typically, the outer pales are attached in pairs or in groups of three to a single inner phyllary such that the phyllary and attached pales surround a ray floret. The shape of the inner pales varies within limits in each species and is a useful taxonomic feature. Pale shape is most variable in *G. quadriradiata* and *G. mandonii.* The ease of detachment of the phyllaries and pales is a useful feature, e.g., these structures remain attached to the receptacle long after the achenes have fallen in *G. parviflora* while in other species pales and phyllaries are readily deciduous.

Receptacle. The size and shape of the receptacle is fairly uniform within each species (with the exception of *Galinsoga parviflora, G. quadriradiata,* and *G. mandonii*) and is a useful character.

Florets. The number of ray and disc florets is of restricted value at the specific level, although the number of florets is a useful feature at the sectional level. The shape and relative size of the ray ligule are similarly reliable features at the sectional level. Color of the ray ligule, however, is not a reliable specific indicator as has been suggested by earlier workers (St. John & White, 1920; Thellung, 1916). The relative lengths of the disc corolla throats and tubes are useful taxonomic features.

Achenes. The achenes of most taxa are dimorphic with the ray achenes being slightly larger, more flattened, and usually curved inward at the base. Achenial size relative to the length of the disc corolla is a useful character, When pubescent, the achenes are strigose with 2- or 3-celled, acute trichomes of the Zwillingshaare type (Hess, 1938) or of 2-4 cells and blunt (as in *Galinsoga triradiata*).

Pappus. Herbarium, and especially field studies, have shown the pappose vs. epappose conditions, length of the pappus, and to some degree, the number of pappus scales, to be of limited diagnostic value. With the exception of the little known *Galinsoga formosa,* all pappose species contain epappose members. It would not be surprising to find in the future that the species now known only from epappose specimens (*G. mollis, G. glandulosa, G. durangen-*

sis, and *G. triradiata*) contain pappose representatives as well. Shape of the pappus scales is relatively stable within each species but is variable in *G. quadriradiata* and *G. mandonii*. The ray achenes often lack a pappus even when the disc achenes are pappose, or the ray pappus is shorter and consists of fewer scales than the disc pappus.

Anthers. Total anther length varies little within species but differs among species. In some species the shape of the apical appendage is of diagnostic value.

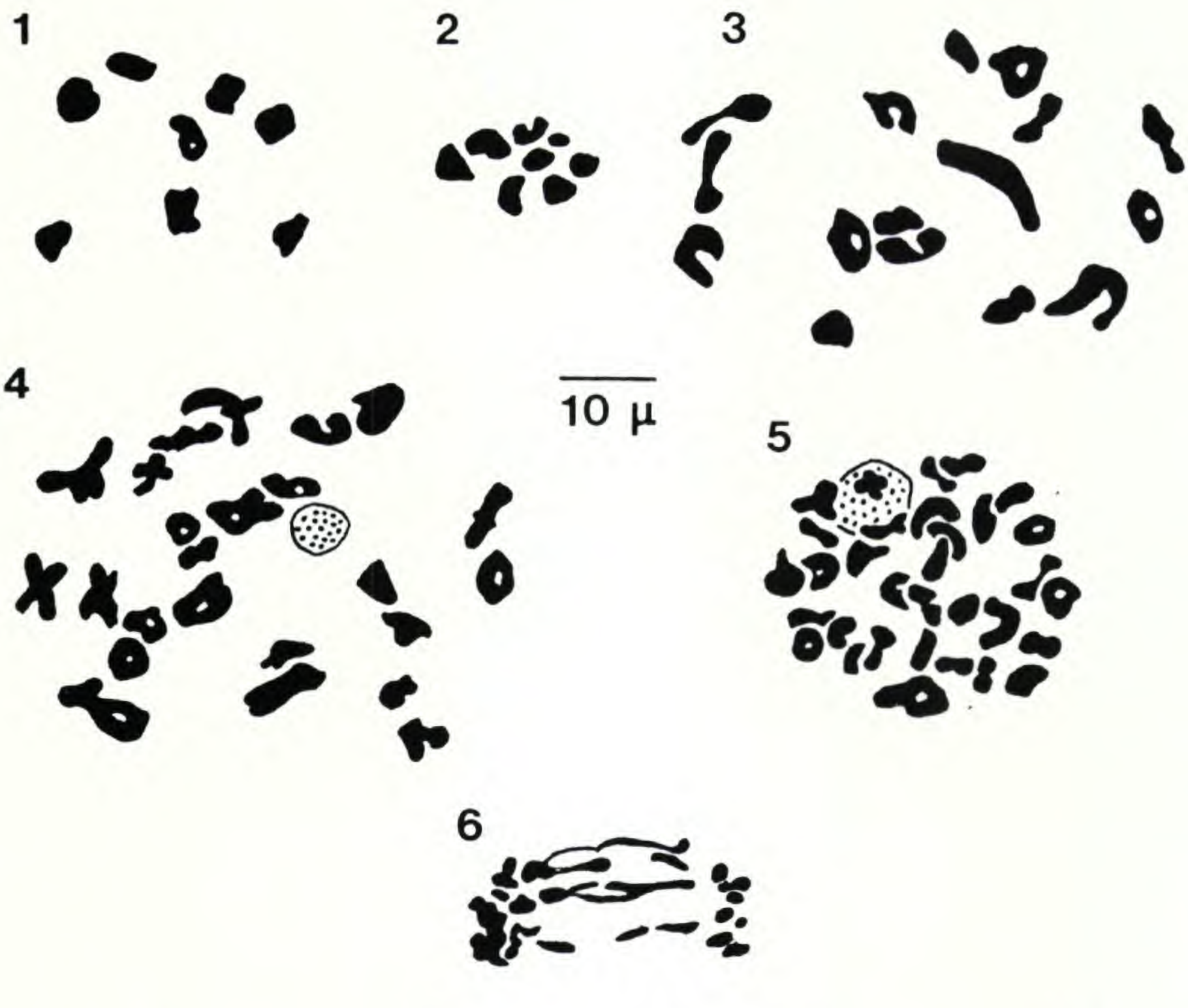
CYTOLOGY

Meiotic chromosome material was collected in the field in Mexico, Guatemala, Peru, and the eastern United States. Buds were killed and fixed in modified Carnoy's solution (4 chloroform : 3 absolute ethanol : 1 acetic acid) and refrigerated until used. Immature florets were stained in acetocarmine solution and slides were prepared using standard squash techniques. Voucher specimens are deposited in The Ohio State University Herbarium (OS).

Chromosome numbers are known for *Galinsoga parviflora* (Figure 1), *G. subdiscoidea* (Figure 2), and *G. quadriradiata* (Figures 3–6) of sect. *Galinsoga*, for *G. filiformis* of sect. *Stenocarpha*, and for *G. elata* and *G. durangensis* of sect. *Elata* (Table 1). The six remaining species of sect. *Galinsoga* and the additional two species of sect. *Elata* are unknown cytologically. Although counts are available for only 43% of the species, all sections have representatives at $n = 8$, and it appears that the base number is $x = 8$.

The count for *Galinsoga subdiscoidea*, $n = 8$, is reported here for the first time. One aneuploid number at $n = 9$ was published for *G. filiformis* by Solbrig, Kyhos, Powell, and Raven (1972) while other authors (Turner, 1965; Turner & Flyr, 1966) list $n = 8$ for this species.

The two widespread weedy species, *Galinsoga parviflora* and *G. quadriradiata*, are the best known cytologically (Table 1). The former taxon has been counted numerous times and apparently is uniformly diploid. The anomalous $n = 18$ count reported by Nawaschin (1926) for *G. parviflora* would seem to be based on a misidentified specimen. Vouchers of *G. parviflora* which I have examined and which were reported in the literature as $n = 16$ have consistently been misidentified specimens of *G. quadriradiata*. An



Figures 1–6. **Camera lucida drawings of meiotic chromosomes of Galinsoga.** 1, *G. parviflora, Canne & Hruschak 91*, $n = 8$. 2, *G. subdiscoidea, Keil & Canne 8917*, $n = 8$. Figures 3–6, *G. quadriradiata:* 3, *Canne 192*, $n = 16$; 4, *Canne 200*, $n = 24$; 5, *Canne 201*, $n = 32$; 6, *Canne 48*, other cells (not shown) same plant $n =$ ca 16. Diakinesis, Figures 1, 3–5; metaphase I, Figure 2; anaphase I with bridges and fragments, Figure 6.

additional problem is that these two species sometimes occur in mixed collections.

Most populations of *Galinsoga quadriradiata* are tetraploid ($n = 16$), though collections from Peru are $n = 24$, and one population was counted as $n = 32$. Many of the tetraploid populations from Mexico and Guatemala show considerable phenotypic variability. Data suggest that these populations differ cytologically as well, for when hybrids are formed meiotic cells frequently contain multivalents and anaphase bridges and fragments (Figure 6). Morphological and chromosomal variation in *G. quadriradiata* is discussed further in the taxonomic section under *G. quadriradiata*.

Table 1. **Chromosome counts in Galinsoga**

Taxon	Chromosome number (*n*)	Reference
G. durangensis (Longpre) Canne		
(as *Tricarpha durangensis*)	8	Keil & Stuessy (1975)
(as *Galinsoga parviflora* and *Sabazia durangensis*)	8	Powell & Sikes (1970) and Urbatsch & Turner (1975), same collection.[1]
(as *Sabazia microglossa* DC.)	8	Turner & Flyr (1966)
G. elata Canne	8	Turner (pers. comm.)
G. filiformis Hemsl.		
(as *Stenocarpha filiformis*)	9	Solbrig, Kyhos, Powell, & Raven (1972)
(as *Stenocarpha filiformis*)	8	Turner & Flyr (1966) and Turner (1965), same collection.[1]
G. quadriradiata Ruiz & Pavon	16	Canne (present paper), 229 plants from 181 populations.[2]
	24	Canne (present paper), 24 plants from 16 populations.[3]
	32	Canne (present paper), 2 plants from 1 population.[4]
(as *G. ciliata*)	ca 16(15)	DeLisle (1965)
(as *G. ciliata*)	16	Haskell & Marks (1952, 1954);[1] Longpre (1970); Solbrig, Kyhos, Powell, & Raven (1972)
(as *G. urticaefolia*)	ca 16	Powell and King (1969)
	16	Skalińska, et al. (1964)[1]
(as *G. parviflora*)	16	Turner & Flyr (1966)
(as *G. urticaefolia* & *G. parviflora*)	16	Turner & King (1964), four collections
(as *G. parviflora*)	ca 16,16	Turner, Powell, & King (1962), six collections
(as *G. ciliata*)	16	van Loon (1974)[1]

G. subdiscoidea Cronq.	8	Canne (present paper), three plants from three populations[2]
G. subdiscoidea × **G. quadriradiata**(?)	24	Canne (present paper), two plants from one population[2]
G. parviflora Cav.	8	Canne (present paper), 59 plants from 50 populations[2]
	8	Chatterjee & Scharma (1968);[1] Covas & Schnack (1946);[1] Diers (1961); Fernandes & Queiros (1971)[1]
(as *G. ciliata*)	8	Gadella (1972);[1] Gadella & Kliphuis (1967);[1] Haskell & Marks (1952, 1954);[1] Koul (1964);[1] Majovský (1970);[1] Mehra, Gill, Mehra, & Sidhu (1965), two collections[1]
G. parviflora	18	Nawaschin (1926)[1]
	8	Pólya (1950)[1]
	ca 8	Powell & King (1969), two collections
	8	Skalińska et al. (1964);[1] Solbrig, Kyhos, Powell, & Raven (1972); Strother (1976);[1] Subramanyam & Kamble (1967);[1] Torres & Liogier (1970); Turner & Lewis (1965); Turner, Powell, & King (1962), two collections

[1]Voucher specimens not examined.
[2]Vouchers for these counts indicated by * in representative specimens.
[3]Vouchers for these counts indicated by † in representative specimens.
[4]Voucher for this count indicated by § in representative specimens.

Based on karyotype analysis, Haskell and Marks (1952) concluded that *Galinsoga quadriradiata* was not a tetraploid derivative of the diploid *G. parviflora* (see also the discussion in the taxonomic section under *G. parviflora*).

PHYLOGENY

The phylogenetic relationships discussed here are based upon morphological, distributional and chromosomal information. Although the scheme proposed in Figure 7 is speculative at best, it is also plausible and thus illustrates a possible phylogeny for the genus. The difficulties inherent in constructing phylogenies are well known (Stebbins, 1974). Additional uncertainties are encountered with *Galinsoga* because several species are known only from a few collections, and some species only from the type collections. In these latter cases particularly, chromosome numbers are unknown and morphological variability is not well documented.

These deficiencies notwithstanding, enough information is available to make the following comments. Because the center of diversity for *Galinsoga* is in Mexico, and the most closely related genera (*Sabazia, Tridax,* and *Selloa*) are also centered in central Mexico (Longpre, 1970; Powell, 1965), it is assumed that *Galinsoga* underwent initial diversification there. Three major lines of divergence appear to have occurred and have led to the presently recognized sections of the genus.

The determination of which of these sections is most similar to the ancestral *Galinsoga* is based partially on the premise that the more primitive section would display its greatest diversity and distribution in central Mexico where the genus is thought to have originated. Second, the taxa in the primitive section could be expected to occupy fairly stable habitats (Stebbins, 1974), in this case mesic sites in or near the pine forest zone in central Mexico. Third, the primitive section would be composed of taxa most similar to species of the genus most closely related to *Galinsoga,* the genus *Sabazia,* because they would presumably share common ancestral features.

Galinsoga sect. *Elata* best meets these criteria. On morphological grounds, *G. formosa* is clearly the species most closely resembling *Sabazia,* followed by *G. elata, G. durangensis,* and *G. mollis.* Sect. *Stenocarpha* is represented by *G. filiformis,* a species of un-

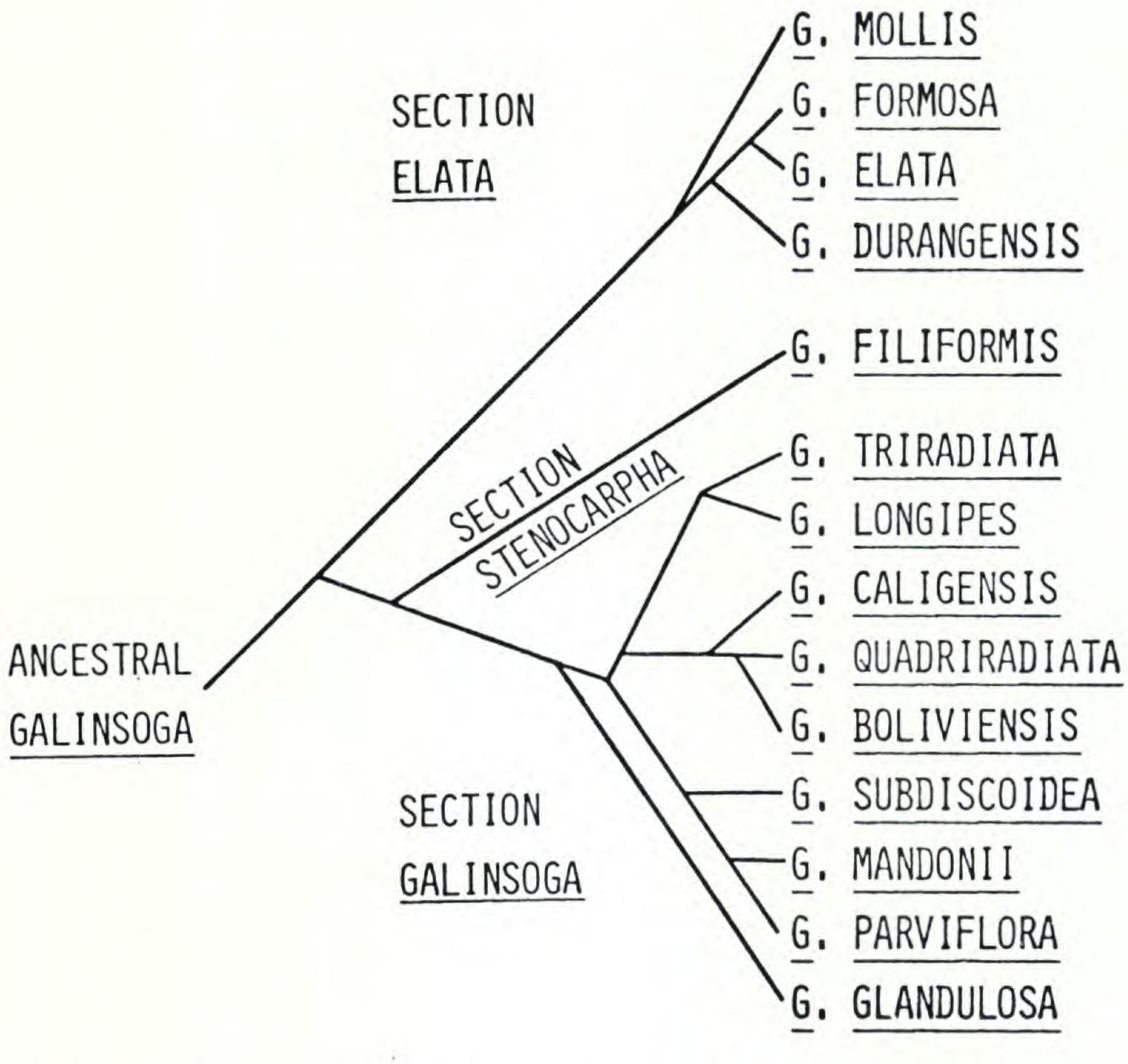


Figure 7. **Proposed phylogeny for Galinsoga.** Amount of branching indicates relative degree of departure from the ancestral *Galinsoga*.

certain affinities which falls morphologically between sect. *Elata* and sect. *Galinsoga*.

Sect. *Galinsoga* is the largest section and contains the most widely distributed species. Three lines of divergence have occurred within the section. *Galinsoga glandulosa* is included in sect. *Galinsoga* because of its habit, leaf features, and capitula characteristics, but it is unique within the section because of a few *Tridax*-like characters. Presumably, these latter characteristics were retained during evolution from that part of the ancestral Galinsoginae complex from which *Tridax* and *Galinsoga* arose.

The line which gave rise to the weedy *Galinsoga quadriradiata* diversified in Mexico, and apparently later in South America. Perhaps *G. triradiata* and *G. longipes* of Mexico came off this line

earlier than the others because these species are more similar to the species in sect. *Elata* than are others in the section. Migration into Central America and South America was followed by the differentiation of *G. caligensis* in the coastal deserts of Peru, and apparently sometime later, by the formation of *G. boliviensis.* This latter species is morphologically more similar to *G. quadriradiata* than is *G. caligensis,* but also, it is not subjected to the extreme environmental conditions and selection pressures of the desert species.

Galinsoga quadriradiata itself is the most variable species in the genus. It is also the only known polyploid member (except for one $n = 9$ count for *G. filiformis,* also known at $n = 8$). Because the chromosome numbers of the other members of the *G. quadriradiata* line are unknown, it is not possible to determine if polyploidy occurred early in the diversification of the line, for example, before it entered South America, or if *G. quadriradiata* is the only taxon in the line to have experienced chromosomal increase.

The remaining three species in sect. *Galinsoga* all have very small ray corollas and may even lack ligules. This *G. parviflora* line apparently originated in Mexico where *G. subdiscoidea* and *G. parviflora* appear to be native. *Galinsoga mandonii,* however, is known only from the Andes of western South America and presumably originated there following the introduction of the *G. parviflora* line into the continent. *Galinsoga parviflora* also occurs in South America but as a weed in cities and agricultural areas, and so it seems to be introduced there.

TAXONOMIC CONCEPTS

The primary criterion employed during this study for delimitation of taxa at all levels was morphological continuity within, and discontinuity among, the taxa. Chromosomal and eco-geographical data were used as well. Because most species of *Galinsoga* are morphologically variable at the inter- and intrapopulational levels, the diagnostic characters chosen here are those features found to be least variable, and these are used in combination to distinguish species. With one notable exception involving *G. subdiscoidea,* little morphological and chromosomal evidence of gene flow exists among species. Presumably the morphological units delineated here are maintained as distinct due to reproductive barriers among them.

TAXONOMY

Galinsoga Ruiz & Pavon, Prod. 110. *t. 24.* 1794. LECTOTYPE SPECIES: *Galinsoga parviflora* Cav.

Wiborgia Roth, Catal. Bot. **2:** 112. 1800. *nom. rejic.* non *Viborgia* Moench. 1794. nec *Wiborgia* Thunberg. 1800. *nom. conserv.* TYPE SPECIES: *Wiborgia acmella* Roth = *Galinsoga parviflora* Cav.

Galinsogea [attributed to Ruiz & Pavon] Willd. Sp. Pl. **3:** 2228. 1803. *Orth. mut.*

Gallinsoga [attributed to Cav.] Jaume St. Hil. Expos. **1:** 417. 1805. *Orth. mut.*

Galinsoja [attributed to Cav.] Roth, Catal. Bot. **3:** 78. 1806. *Orth. mut.*

Vigolina Poiret in Lamarck, Encycl. Meth. **8:** 613. 1808. Substitute name for *Wiborgia* Roth. *nom. rejic.*

Galinsogaea [attributed to Ruiz & Pavon] Zucc. Flora **4:** 612. 1821. *Orth. mut.*

Galinsogea [attributed to Ruiz & Pavon] Spreng. Syst. Veg. **3:** 579. 1826. *Orth. mut.*

Galinzoga [attributed to Cav.] Dumort. Fl. Belg. 72. 1827. *Orth mut.*

Vargasia DC. Prodr. **5:** 676. 1836. non Bertero ex Spreng. 1825. *nom. illegit.* TYPE SPECIES: *Vargasia caracasana* DC. = *Galinsoga quadriradiata* Ruiz & Pavon.

Adventina Raf. New Fl. N. Amer. **1:** 67. 1836. LECTOTYPE SPECIES (here designated): *Adventina parviflora* Raf. = *Galinsoga parviflora* Cav.

Stemmatella Wedd. ex Benth. in Benth. & Hooker, Gen. Pl. **2:** 193, 359, 360. 1873. TYPE SPECIES: *Stemmatella congesta* Wedd. ex O. Hoffm. = *Galinsoga mandonii* Sch.-Bip.

Galinsogaea [attributed to Cav.] Himpel, Fl. Elsass-Lothr. 187. 1891. *Orth. mut.*

Stenocarpha S. F. Blake, Bull. Misc. Inform. 1915. 348. 1915. TYPE SPECIES: *Stenocarpha filiformis* (Hemsl.) S. F. Blake = *Galinsoga filiformis* Hemsl.

Annual herbs. Stems erect or decumbent, striate, green to red, sparsely to densely pilose with multicellular trichomes. Leaves opposite, sessile or petiolate, the petioles narrowly connate around the stem; blades elliptic to broadly ovate, nearly glabrous to densely pilose on both surfaces, with 3 principal veins, at the apex acute to acuminate, at the base rounded, cuneate or attenuate. Peduncles slender, pilose. Heads in loose to congested cymose clusters. Involucre 1–3 seriate, hemispherical to narrowly campanulate; outer phyllaries 1–4, herbaceous, triangular to elliptic, flattened or convex, glabrous or sparsely short pilose, at the apex acute to obtuse, with the margins entire or minutely laciniate and sometimes scarious; inner phyllaries herbaceous or scarious, narrowly to broadly ovate or lanceolate-ovate, glabrous or sparsely pilose, at the apex acute or obtuse, with the margins entire, ciliate or minutely lacini-

ate. Receptacle broadly to narrowly conical. Pales usually dimorphic, scarious, with conspicuous veins; outer pales lanceolate, elliptic or broadly ovate, entire to trifid, convex, at the apex acute to obtuse, sometimes purple or red, with the margins minutely laciniate above the middle; often joined in groups of 2–3 at the base to a single phyllary and these together enclosing a ray floret; inner pales linear to narrowly ovate, convex to conduplicate, entire to deeply trifid, at the apex acute or obtuse, rarely weakly cuspidate. Ray florets 3–15, usually 5–8, rarely lacking, fertile, with corollas white to purple; ligules ovate, obovate to oblong, usually trilobed, rarely bilabiate; tubes pilose; style bifid; achenes black, obconical or obpyramidal, usually somewhat flattened and curved inward at the base, glabrous or strigose, pappose or epappose. Disc florets 5–150, fertile, corollas yellow, greenish-yellow or rarely purple; throats cylindrical, rarely campanulate, pilose or rarely glabrous; lobes 5, acute, papillose, erect or recurved; tubes minutely pilose; anthers yellow or brown, with ovate to oblong apical appendages, at the base sagittate; style branches recurved, somewhat flattened, at the apex acute; achenes black, obconical to obpyramidal, subterete, glabrous or strigose, epappose or with a pappus of lanceolate, laciniate or fimbriate, obtuse to aristate scales, or rarely of setose bristles. Chromosome numbers, $x = 8$ ($n = 8, 16, 24, 32$).

KEY TO SPECIES

A. Ray florets 8–15; ligules 3–12 mm long; disc corollas with throats 1.5–2.5 mm long. ..... B.
  B. Leaves cauline and basal; inner pales linear, entire, 0.2–0.4 mm wide; achenes 0.5–0.8 mm long. ..... 5. *G. filiformis.*
  B. Leaves cauline; inner pales lanceolate and trifid or linear-oblong and entire, or with 1–2 short, lateral lobes, 0.4–3.5 mm wide; achenes 1–1.5 mm long. ..... C.
    C. Plants 100–150 cm tall; leaves entire or with margins remotely denticulate; inner pales linear and entire or with 1–2 short, lateral lobes. ..... 4. *G. mollis.*
    C. Plants to 75 (–100) cm tall; leaf margins serrate; inner pales deeply trifid. ..... D.
      D. Phyllaries and outermost pales attached at the base and enclosing the ray florets; ligules conspicuously trifid; pappus of fimbriate scales or lacking. ..... 2. *G. elata.*
      D. Phyllaries and outermost pales separate, not enclosing the ray florets; ligules shallowly tridentate; pappus of caducous seta or lacking. .... E.
        E. Ligules 1–1.2 cm long; disc corollas with throats 1.5–1.8 mm long; pappus of caducous seta. ..... 1. *G. formosa.*

E. Ligules 0.3–0.7 cm long; disc corollas with throats 1.7–2.5 mm long; pappus lacking. ..... 3. *G. durangensis.*

A. Ray florets 0–5; ligules absent or to 6 mm long; disc corollas with throats 0.7–1.6 mm long. ..... F.

F. Involucre uniseriate; pales with conspicuously ciliate margins; anther appendages with 1 or 2 multicellular glands. ..... 14. *G. glandulosa.*

F. Involucre biseriate; pales with minutely laciniate margins; anther appendages without glands. ..... G.

G. Heads usually 4–15 mm wide; ligules 2–7 mm wide, 3 lobed, the lobes conspicuous and about equal. ..... H.

H. Ligules usually 3–6 mm long; ray achenes 1–1.4 mm long. ..... I.

I. Ray florets 5; ligules 2–3.5 mm wide; inner pales lanceolate, entire or with 1–2 short, lateral lobes; achenes strigose with acute trichomes or glabrous. ..... 6. *G. longipes.*

I. Ray florets 3 (–5); ligules 4–7 mm wide; inner pales linear-obovate, entire; achenes with blunt trichomes or glabrous. ..... 7. *G. triradiata.*

H. Ligules 0.9–3.8 mm long; ray achenes 1.3–2.3 mm long. ..... J.

J. Plants usually 20–62 cm tall; leaf margins serrate; outermost pales 2–3 mm long. ..... 9. *G. quadriradiata.*

J. Plants usually 3–15 cm tall; leaf margins entire or sometimes serrulate; outermost pales 3–4 mm long. ..... K.

K. Heads 8–10 mm wide; ligules 2–3.8 mm long; outer row of disc florets pistillate; ray achenes 1.4–1.7 mm long. ..... 8. *G. caligensis.*

K. Heads 4–7 mm wide; ligules 1.4–2.3 mm long; all disc florets perfect; ray achenes 2–2.3 mm long. ..... 10. *G. boliviensis.*

G. Heads usually 1.5–5 mm wide; ligules absent or 0.2–2 mm wide, 1–3 lobed, the lobes short and unequal. ..... L.

L. Leaves elliptic to oblanceolate; inner pales entire or with 1–2 short, lateral lobes; disc corollas greenish-yellow with cupulate throats; pappus of spathulate yellow scales. ..... 11. *G. subdiscoidea.*

L. Leaves ovate to lanceolate; inner pales trifid; disc corollas deep yellow to reddish-purple with cylindrical throats; pappus of lanceolate, obtuse to aristate, white or gray scales or absent. ..... M.

M. Heads usually sessile; phyllaries reddish-purple; ray corollas white to reddish-purple; phyllaries and pales deciduous. . 12. *G. mandonii.*

M. Heads on peduncles 0.1–4 cm long; phyllaries green; ray corollas dull white or rarely pink; phyllaries and pales persistent. ..... 13. *G. parviflora.*

I. **Galinsoga** section **Elata** Canne, sect. nov.

Plantae 0.25–1.5 m altae; folia caulina; pedunculi (0.5–) 1.5–8.2 cm longi, graciles; capitula in cymis laxis; paleae interiores lanceolatae et trifidae vel anguste obovatae et integrae-aliquanto trifidae, 0.4–1.5 (–3.5) mm latae; flosculi radii 8–13 (–15), ligulis (3–) 4–12

mm longis, obovatis-oblongis; flosculi disci (30–) 50–150, faucibus corollarum 1.5–2.5 mm longis. TYPE SPECIES: *Galinsoga elata* Canne.

1. **Galinsoga formosa** Canne, nom. nov.

Sabazia trifida Fay, Brittonia **25:** 197. *t. 4.* 1973. TYPE: **Mexico:** Oaxaca, Sierra Madre del Sur, ca 125 km S of Oaxaca, on rd to Puerto Angel, 8 Nov 1970, *A. Cronquist & J. Fay 10889* (Holotype, NY!; isotypes, CAS, DUKE, ENCB, F, GH, KANU, MEXU, MICH! MSC, S, TEX, US, UTC). The specific epithet "trifida" is not used here because of the earlier publication by Persoon (1807) of *Galinsoga trifida*.

Annual herbs, to ca 1 m tall. Stems sparsely to moderately pilose with spreading to retrorse, multicellular trichomes to 1.5 mm long. Leaves with petioles 1–25 mm long; blades lanceolate-rhomboid to lanceolate-ovate, 2–6(–11) cm long, 0.5–3(–5.5) cm wide, with both surfaces hirsute, at the apex acute to acuminate, at the base cuneate to rounded, margins serrate, ciliate. Peduncles to 5 cm long, pilose. Heads to 0.8 cm tall, to 2.2 cm wide. Involucre 3-seriate, hemispherical; outer phyllaries lanceolate-ovate to rhomboid, 3.2–6.1 mm long, 1–2 mm wide, pilose, at the apex acute, with the margins ciliate; inner phyllaries elliptic to lanceolate, herbaceous to scarious, to 5 mm long, to 3 mm wide, sparsely pilose, at the apex acute to obtuse, with the margins ciliate. Receptacle conical. Pales 3–5 mm long, deeply bifid or trifid. Ray florets (8–)10–15, with corollas white, often purple below; ligules oblong, 1–1.2 cm long, to ca 0.3 cm wide; tubes ca 2.5 mm long; achenes narrowly obconical, 1.2 mm long, 0.5 mm diam, glabrous; pappus of 3–5 caducous seta, 1–2 mm long. Disc florets ca 100, with throats 1.5–1.8 mm long, 0.7 mm diam, minutely pilose near the base, with the lobes 0.3–0.4 mm long; tubes 1–1.2 mm long; anthers ca 1 mm long, with the appendage ovate and bearing 2 multicellular glands; achenes like those of the ray florets. Chromosome number unknown.

DISTRIBUTION. Known only from the type collection from steep, gravelly banks in the pine-oak-alder zone of the Sierra Madre del Sur, Oaxaca, Mexico, ca 2400 m. Figure 8.

Fay (1973), who originally described this taxon as *Sabazia trifida,* commented that it was included in *Sabazia* as "a somewhat anomalous species" because it combined deeply trifid pales, shallowly lobed ligules, and a setiform pappus. The first two of these char-

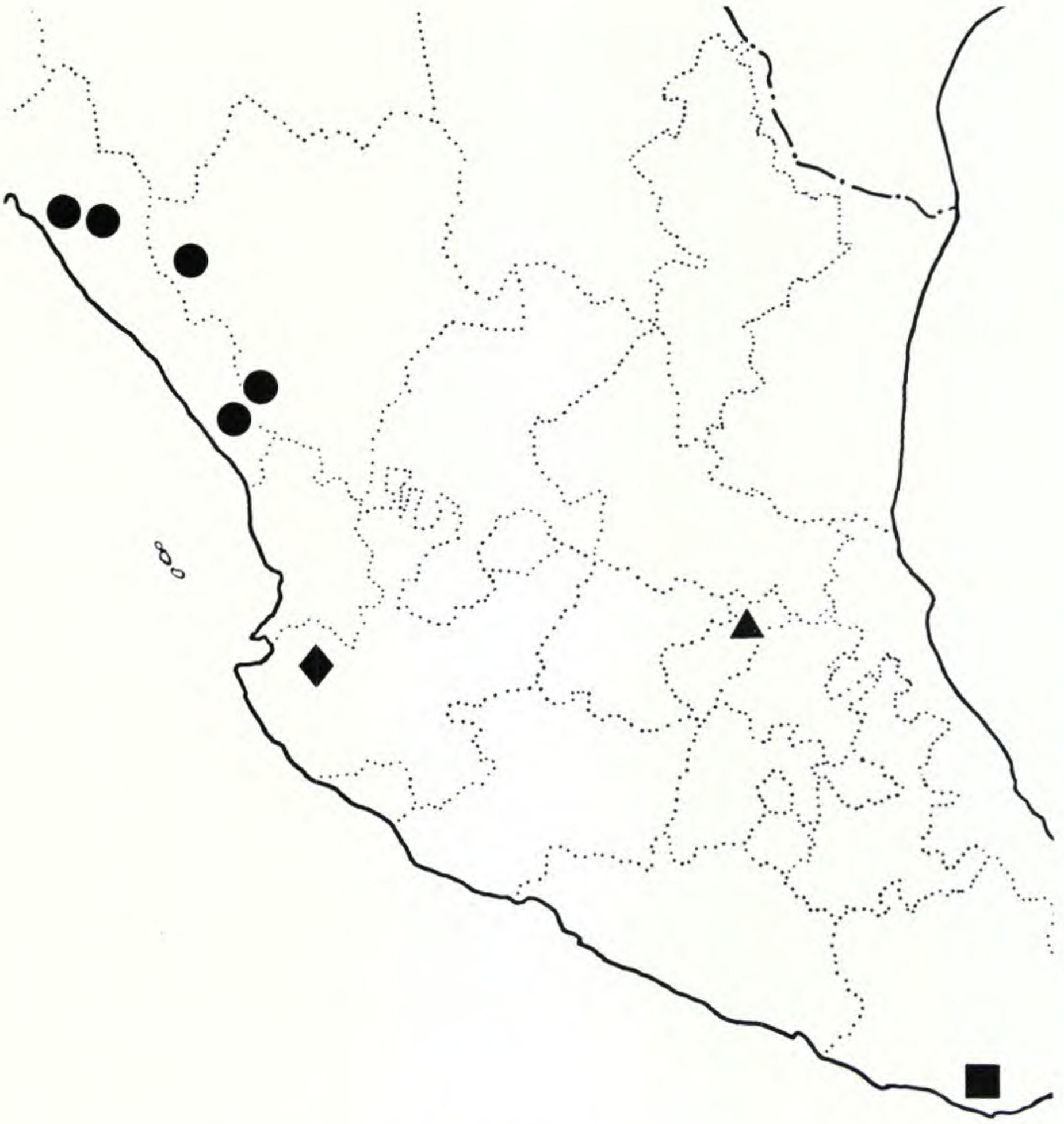


Figure 8. **Mexican distributions of Galinsoga.** Map of Mexico indicating the distributions of *Galinsoga durangensis* (dots), *G. elata* (triangle), *G. formosa* (square), and *G. mollis* (diamond).

acters were used to distinguish the genus *Tricarpha* (Longpre, 1970) and the third feature was unknown in *Sabazia,* but it occurred in the related genus *Selloa.* Shallowly lobed ligules and trifid pales are common in *Galinsoga,* but *G. formosa* is the only species to possess a setiform pappus.

This species is transferred to *Galinsoga* because it is an annual with a slender taproot typical of *Galinsoga,* whereas *Sabazia* is primarily a genus of perennials arising from caudices. In features of leaves, stems, and capitulescence the taxon is very similar to the

other species of *Galinsoga* sect. *Elata,* especially *G. elata* (under which see discussion). Finally, the achenes, pales, anthers, and lobing of the ray ligule resemble those found in various species of *Galinsoga* from all three sections. The specific epithet, *formosa,* was chosen because of the attractiveness of this species.

2. **Galinsoga elata** Canne, sp. nov. Figure 9.

Herbae annuae, usque ad 75 cm altae. Caules internodiis usque 10.5 cm longis, virides-rubri vel rubri, sparse vel modice pilosi. Folia petiolis 2–15 mm longis; laminae elongatae ovatae vel lanceolatae, 2–7 cm longae, 0.6–3 cm latae, sparse vel modice pilosae utrinque, apice acuto-acuminato, basi rotundata usque cuneata; margines serrulati-serrati. Pedunculi 0.9–8.2 cm longi. Capitula 5–8 mm alta, 9–20 mm lata. Involucrum biseriatum, hemisphaericum; phyllaria exteriora covexa, elliptica-lanceolata, 2.2–4 mm longa, 1–2 mm lata, pilosa, trichomatibus glandulosis et eglandulosis, apice acuto vel obtuso, marginibus anguste scariosis, integris vel minute laciniatis; phyllaria interiora parabolica vel lanceolata-ovata, usque ad 5 mm longa et 2.5 mm lata, glabra vel pilosa, apice obtuso, marginibus scariosis, purpureis-laciniatis. Receptaculum 3–3.8 mm altum, 2.2–2.3 mm diametro. Paleae extimae ellipticae-lanceolatae, 3–3.5 mm longae, 1.2–1.5 mm latae, integrae vel bilobatae, junctae ad basim binatim et terni ad phyllarium contiguum; paleae interiores lanceolatae, 2.1–3 mm longae, 0.7–1.5 mm latae, profunde trifidae. Flosculi radii 8, corollis albis vel purpureis; ligulae quadratae vel obovatae, 4.5–6 mm longae, 3.5–4.5 mm latae, brevipilosae in venis dorsalibus, lobis obtusis, 1–2 mm longis; tubi 1–1.5 mm longi; achenia obconica, aliquantum complanata, 1.5 mm longa, strigosa vel glabra; pappi absentes vel squamellae ca 7, adaxiales, obtusae, fimbriatae, ca 0.5 mm longae. Flosculi disci 75–120, corollis luteis; fauces 1.5–1.6 mm longae, 0.8–1 mm diametro, lobis 0.3–0.5 mm longis; tubi 0.5–0.8 mm longi; antherae brunneolae, 0.9–1 mm longae, appendice anguste ovata; achenia obconica, aliquantum angulata, 1.1–1.5 mm longa, 0.3–0.5 mm diametro, strigosa vel glabra; pappi absentes vel squamellae 15–20, obtusae, fimbriatae, 0.6–1.2 mm longae. Chromosomatum numerus: $n = 8$.

TYPE: **Mexico:** Querétaro, ca 1.5 mi E of Pinal de Amoles, rd between Vizarrón and Jalpan, 21° 10′N, 99° 38′W, 7200 ft, 8 Nov

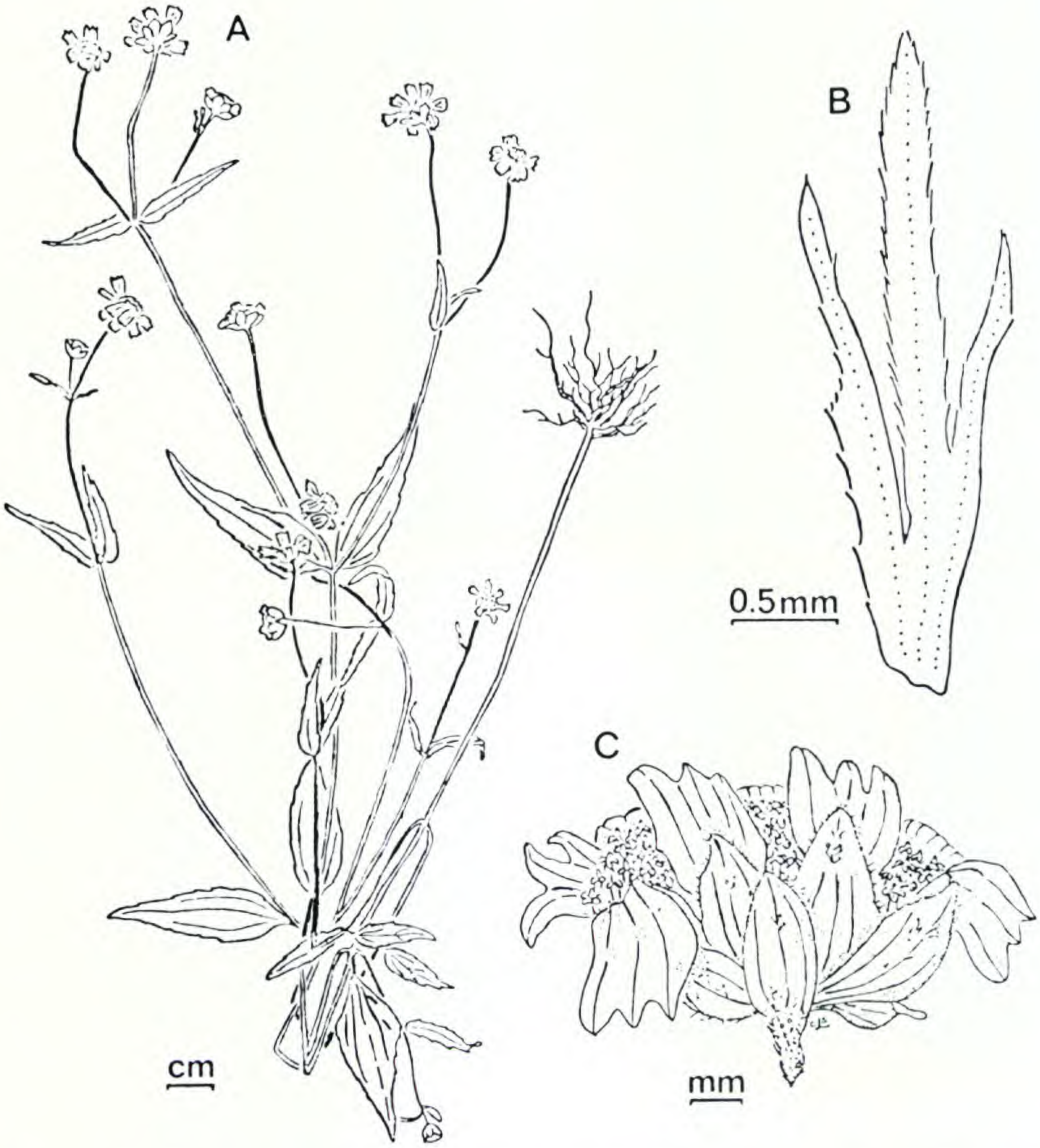


Figure 9. **Galinsoga elata.** A, habit; B, inner pale; C, head. All *Webster & Breckon 16302;* A (OS), B and C (MICH).

1970, *G. L. Webster & G. J. Breckon 16302* (Holotype, DAV!; isotypes, MICH! OS!).

DISTRIBUTION. *Galinsoga elata* is known only from the type locality, where the species is common on gray metamorphic rock in wet steep places along the highway.

In terms of overall morphology, *Galinsoga elata* appears close to *G. formosa.* Although the leaf surfaces of *G. formosa* are more densely pilose than in *G. elata,* leaf shape is similar. The peduncles, capitulescence, and inner pales are similar, and both species have

large heads containing numerous disc florets. The species differ most dramatically in that *G. elata* has a pappus of short scales and aglandular anther appendages, whereas *G. formosa* has a setose pappus and anther appendages with 2 multicellular glands. The species is named for its attractive tall stature.

SPECIMENS EXAMINED. **Mexico.** QUERETARO: 1.5 mi E of Pinal de Amoles, *Turner 76–9* (OAC, OS).

3. **Galinsoga durangensis** (Longpre) Canne, comb. nov.

Tricarpha durangensis Longpre, Publ. Mus. Michigan State Univ., Biol. Ser. **4**(8): 378. 1970. TYPE: **Mexico:** Durango, Mexico hwy 40, 7.5 mi ENE Revolcaderos, 7200 ft, 7 Nov 1964, *D. Flyr 292* (Holotype, MSC!; photograph of holotype, MSC!; isotype, TEX).

Sabazia durangensis (Longpre) Urbatsch & Turner, Brittonia **27:** 351. 1975.

Annual herbs to 66 cm tall. Stems with internodes to 17 cm long. Leaves with petioles 0.2–1.6 cm long; blades ovate to narrowly lanceolate, 1.2–8 cm long, 0.5–3.7 cm wide, at the apex acute to acuminate, at the base cuneate to rounded, with both surfaces sparsely to moderately pilose; margins sharply serrate to serrulate and ciliate. Peduncles 0.5–6.5 cm long, moderately to densely appressed to spreading pilose, sometimes with glandular capitate trichomes intermixed, often furnished with one or a pair of linear, pilose bracts, 2–4 cm long, 0.5–1 cm wide. Heads 0.3–0.7 cm tall, 0.7–2 cm wide. Involucre 2–3 seriate, campanulate to hemispherical, glabrous or sparsely glandular pilose; outer phyllaries ovate to oblong-elliptic, 2.5–4 mm long, 1.2–1.8 mm wide, with the margins scarious, hyaline or purple, minutely laciniate-ciliate; inner phyllaries narrowly ovate, 2–4.5 mm long, 0.6–1.2 mm wide, somewhat convex, at the apex attenuate. Receptacle 1–2 mm tall, 1–2 mm diam. Pales 1.8–3.5 mm long, deeply trifid. Ray florets 8–13; ligules rectangular to cuneate-oblong, 3–7 mm long, 1.3–4 mm wide, glabrous or sparsely and minutely pilose dorsally, with the lobes obtuse, 0.2–1 mm long; tubes 1–2 mm long; achenes narrowly obconical, 1.2 mm long, 0.4–0.5 mm diam, glabrous, epappose. Disc florets 30–65; throats 1.7–2.5 mm long, 1 mm diam, minutely pilose; lobes 0.5 mm long; tubes 0.6–0.7 mm long; anthers 1 mm long, with appendages narrowly ovate; achenes like those of the ray florets. Chromosome number, $n = 8$.

DISTRIBUTION. Known from Sinaloa and neighboring Durango, Mexico, in moist ravines and along north-facing slopes in the pine-oak zone (Figure 8), 300–2400 m. Flowering from September to November.

This species appears to be an annual (rather than perennial as reported by Longpre, 1970) with a slender taproot and many secondary fibrous roots.

One specimen, *Ortega 4456,* differs from the others by having smaller heads, fewer florets per head and glandular capitate trichomes on the peduncles. All three of these features are known to vary in several other species, and it is likely that the *Ortega* specimen is an indication that the imperfectly known *Galinsoga durangensis* also shows the morphological variability recorded elsewhere in the genus.

The recent recognition of several new species (Fay, 1973; McVaugh, 1972; and the present paper) has dissolved the generic boundaries reported by Longpre (1970) for *Tricarpha.* Deeply trifid pales, scarious phyllary margins, and shallowly lobed ray corollas were features used as generic markers for *Tricarpha* (Longpre, 1970). All of these characters are present, either singly or in various combinations, in many species of *Galinsoga* (e.g., *G. parviflora, G. triradiata,* and *G. longipes* of sect. *Galinsoga, G. filiformis* of sect. *Stenocarpha, G. elata, G. formosa,* and *G. mollis* of sect. *Elata*). In addition, Urbatsch and Turner (1975) have pointed out that at least two species of *Sabazia, S. humilis* (HBK.) Cass. and *S. multiradiata* (Seaton) Longpre, also have deeply trifid pales and a few species have scarious phyllary margins.

Galinsoga durangensis has no vegetative or floral features which would exclude it from *Galinsoga,* and in addition has the acute, serrate leaves, small achenes, and large heads on long peduncles characteristic of the species of *Galinsoga* sect. *Elata.* Although *Tricarpha durangensis* is properly transferred to *Galinsoga, T. purpusii* (Brandg.) Longpre with its sharply acute phyllaries in 3 or 4 series, long disc and ray corollas, long anthers, and shiny achenes seems best moved to *Sabazia,* a course recently followed by Urbatsch and Turner (1975).

SPECIMENS EXAMINED. **Mexico.** DURANGO: La Bajada Tamazula, *Ortega 4456* (US). SINALOA: 5 mi NE of La Cienega, *Breedlove & Kawahara 17044* (MICH); below

Buenas Juntas, 5 mi NW of Los Ornos, *Breedlove & Thorne 18222* (MICH); 21.9 mi NE of Santa Lucia, *Keil & Canne 8860* (OS).

4. **Galinsoga mollis** McVaugh, Contr. Univ. Michigan Herb. **9:** 414. *t. 26.* 1972. TYPE: **Mexico:** Jalisco, 20–22 km S of Talpa de Allende, headwaters of a west branch of Rio de Talpa, 1200–1450 m, 28–30 Mar 1965, *McVaugh 23300* (Holotype, MICH!; isotypes, DUKE! ENCB! NY!).

Annual (?) herbs to 1.5 m tall. Stems green to reddish-green, pilose with short trichomes to 0.3 mm long, intermixed with trichomes to 2 mm long. Leaves with petioles to 1.5 cm long or sessile to subsessile, sometimes alternate near the capitulescence; blades elliptic-lanceolate, 1–15 cm long, 0.5–4 cm wide, at the apex acuminate, at the base attenuate to rounded, with both surfaces pilose; margins remotely denticulate. Peduncles 1.5–4.5 cm long, densely appressed pilose. Heads 0.6–0.9 cm tall, 1.5–2 cm wide. Involucre subglobose, 2–3 seriate, glabrous, outer phyllaries narrowly to broadly ovate, flattened, 1.5–3.5 mm long, 1.2–3 mm wide; innermost phyllaries broadly elliptic, ovate to slightly obovate, convex, 3–3.8 mm long, 2–2.8 mm wide, at the apex obtuse, with the margins scarious. Receptacle 1.5–2.8 mm tall, 2–2.5 mm diam. Pales narrowly oblong, convex, entire or with 1–2 short lateral lobes, at the apex obtuse or sometimes acute, outermost pales to 3.5 mm long, to 1 mm wide, joined at the base in pairs to an adjacent phyllary; inner pales to 3 mm long, 0.4–0.6 mm wide. Ray florets 8; ligules obovate, 4–8 mm long, 2.5–4 mm wide, with the lobes acute to obtuse; tubes 2 mm long; achenes obpyramidal, 1.2–1.5 mm long, 0.6 mm diam, dorsally convex, ventrally angular, glabrous, at the apex truncate, epappose. Disc florets 125–150; throats 2 mm long, 1 mm diam, with the lobes 0.5 mm long; tubes 1 mm long; anthers to 1.2 mm long, with the appendage narrowly ovate; achenes obconical, angular, 1–1.3 mm long, 0.5 mm diam, glabrous, epappose. Chromosome number unknown.

DISTRIBUTION. Known only from steep mountainsides in the pine forest of Jalisco, Mexico, where it is abundant at the type locality. Figure 8.

Galinsoga mollis was the first of the tall-statured, large- and few-headed Galinsogas to be recognized (McVaugh, 1972). Until

the present work it has existed as an unusual species in a genus traditionally characterized by small herbs with numerous heads only a few millimeters in diameter. However, as the genus is presently perceived, *G. mollis* falls clearly into sect. *Elata* where it shares the features of many disc florets, long ray ligules and few-headed capitulescence with the other taxa.

The size and soft pubescence of *Galinsoga mollis* remain unique in the genus, and this species is the only member of sect. *Elata* that lacks deeply trifid pales. Morphologically, *G. mollis* seems more remote from the other three species in the section than these latter species do from each other.

II. **Galinsoga** section **Stenocarpha** (S. F. Blake) Canne, comb. et stat. nov.

Stenocarpha S. F. Blake, Bull. Misc. Inform. no. **7:** 348. 1915.

Plantae 10–40 cm altae; folia caulina et basalia; pedunculi 0.5–10 cm longi, filiformes; capitula in cymis laxis; paleae interiores lineares, integrae, 0.2–0.4 mm latae; flosculi radii 8–10, ligulis 2.6–4.5 mm longis, rectangularibus; flosculi disci ca 66, faucibus corollarum 0.7–1.1 mm longis. TYPE SPECIES: *Galinsoga filiformis* Hemsl.

5. **Galinsoga filiformis** Hemsl. Diagn. Pl. Nov. **2:** 34. 1879.
TYPE: **Mexico:** Sinaloa, Cerro de Pinal, Dec 1848, *Seemann 1473* (Holotype, K!).

Stenocarpha filiformis (Hemsl.) S. F. Blake, Contr. Gray Herb. **52:** 57. 1917.
Stenocarpha filipes S. F. Blake, Bull. Misc. Inform. no. 7: 348. 1915.[1]

Stenocarpha filiformis (Hemsl.) S. F. Blake var. *genuina* S. F. Blake, Contr. Gray Herb. **52:** 57. 1917. *nom. illegit.*, based on the type of *Galinsoga filiformis* Hemsl.

Galinsoga filiformis Hemsl. var. *epapposa* Robins., Proc. Am. Acad. Arts **43:** 42. 1907. TYPE: **Mexico:** Durango, San Ramón, 21 Apr-18 May 1906, *E. Palmer 127* (Holotype, GH!; isotypes, MO! NY! UC! US!).

Stenocarpha filiformis (Hemsl.) S. F. Blake var. *epapposa* (Robins.) S. F. Blake, Contr. Gray Herb. **52:** 57. 1917.

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[1]When Blake (1915) first established *Stenocarpha* and made the transfer from *Galinsoga*, he mistakenly used the epithet *filipes*. The correction was made by Blake when he published the name *S. filiformis*.

Annual herbs, 10–40 cm tall. Stems erect, branches sparsely pilose. Leaves sessile or with petioles to 8 mm long, blades at the apex acute to obtuse, at the base attenuate; margins entire or minutely denticulate; blades of basal leaves broadly to narrowly elliptic or obovate, 0.8–4 cm long, 0.5–2.3 cm wide, with the upper surface green or reddish and pilose, with the lower surface green and glabrous to sparsely pilose; cauline leaves sessile or with petioles to 3 mm long, blades narrowly ovate to narrowly elliptic, 1.5–6 cm long, 0.2–1.4 cm wide, with both surfaces glabrous to sparsely pilose. Peduncles 0.5–10 cm long, filiform, sparsely to densely pilose, often subtended by narrowly elliptic bracts, 3–10 mm long, 1–2 mm wide, at the apex acute to obtuse, at the base attenuate. Heads 1.8–4.3 mm tall, 5–8.5 mm wide. Involucre campanulate; outer phyllaries 3, narrowly ovate, 1–2.2 mm long, 0.3–1.3 mm wide, glabrous, at the apex obtuse; inner phyllaries ovate to narrowly ovate, 1.6–2.7 mm long, 0.8–1.5 mm wide, glabrous, at the apex acute to obtuse, with the margins minutely laciniate and narrowly scarious. Receptacle narrow, 1.5–2.6 mm tall, 0.6–1.5 mm diam. Pales linear to linear-obovate, 2–2.5 mm long, 0.2–0.4 mm wide, entire, at the apex acute. Ray florets 8–10, corollas white; ligules rectangular, 2.6–4.5 mm long, 1.2–1.6 mm wide, with the lobes 0.3 mm long, obtuse; tubes 0.6–0.7 mm long; achenes subterete to somewhat angular, 0.5–0.8 mm long, 0.2–0.3 mm diam, glabrous and epappose or strigose and with a pappus of 5 obtuse, fimbriate scales alternating with 5 aristate scales to 0.7 mm long. Disc florets ca 66, throats 0.7–1.1 mm long, 0.4–0.7 mm diam; tubes 0.3–0.6 mm long; anthers 0.5–0.8 mm long, with the appendage ovate; achenes like those of the ray florets. Chromosome numbers, $n = 8, 9$.

DISTRIBUTION. Restricted to the states of Sinaloa and Durango, Mexico (Figure 10), 300–1700 m. Flowering from September to May.

The paucity of cauline leaves and the presence of basal leaves occur regularly only in *Galinsoga filiformis*. The only collection known to have abundant cauline leaves is the progeny of *Breedlove 1668* grown in a greenhouse. Elsewhere in the genus I have seen basal leaves only in greenhouse plants grown from a Mexican collection of *G. quadriradiata* (*Keil & Canne 9179*).

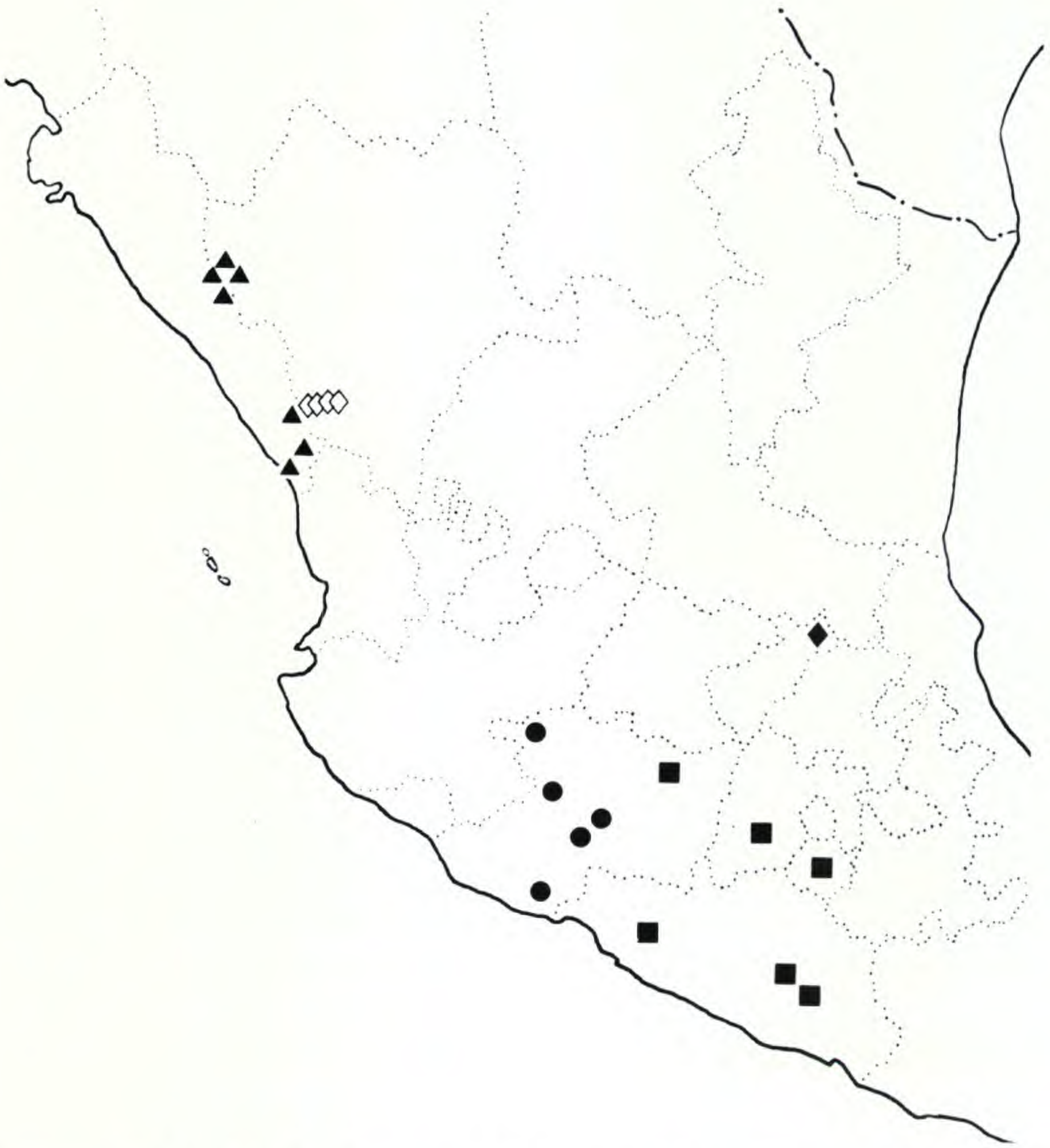

Figure 10. **Mexican distributions of Galinsoga.** Map of Mexico indicating the distributions of *Galinsoga filiformis* (triangles), *G. glandulosa* (solid diamond), *G. longipes* (squares), *G. subdiscoidea* (open diamonds), and *G. triradiata* (dots).

Galinsoga filiformis is placed in a separate section because it is a morphologically well defined taxon which shows no obvious close relationship with any other species. *Galinsoga filiformis* is the only species in the genus with the pales less than 0.4 mm wide, filiform peduncles, narrowly ovate phyllaries, and basal leaves. It was the occurrence of these unique character states which prompted S. F. Blake (1915) to establish the genus *Stenocarpha* for *G. filiformis* Hemsl. However, except for the basal leaves, these character states are quantitative extensions of characters found within *Galinsoga*.

Other features are shared with several members of sect. *Galinsoga* and sect. *Elata*. *Galinsoga filiformis* has the small head size and habit of taxa in sect. *Galinsoga* but possesses the long peduncles, ray corolla number and shape of species in sect. *Elata*.

REPRESENTATIVE SPECIMENS: **Mexico.** DURANGO: La Bajada, municipality of Tamazula, *Ortega 628* (MEXU); La Bajada, Tamazula, *Ortega 4427* (GH, US). SINALOA: Cofradía, near Culiacán, 26 Oct 1904, *Brandegee s.n.* (US), 28 Oct 1904, *Brandegee s.n.* (UC), 31 Oct 1904, *Brandegee s.n.* (GH); Rosario, ca 33 mi E of Concordia, *Breedlove 1668* (DS); Mesa Malquesón, Cerro Colorado, *Gentry 5139* (UC); Capadero, Sierra Tacuichamona, *Gentry 5584* (GH); Manzanitla, *Ortega 901* (US); Rosario, Cacalotán, *Ortega 7134* (F, US); vicinity of Rosario, *Rose, Standley, & Russell 14607* (US).

III. **Galinsoga** section **Galinsoga.**

Galinsoga Ruiz & Pavon, Prodr. 110. *t. 24.* 1794. TYPE SPECIES: *Galinsoga parviflora* Cav.

Plants 1.5–75 cm tall; leaves cauline; peduncles absent to 5(–7) cm long, slender; heads in tight to open cymose clusters; inner pales narrowly obovate and entire to broadly lanceolate and bifid to trifid, 0.3–1.5 mm wide; ray florets 0–5(–9), with ligules absent or to 6 mm long, 0–3.5 mm wide, quadrate to obovate; disc florets 5–70(–100), with corolla throats 0.7–1.6 mm long.

6. **Galinsoga longipes** Canne, sp. nov. Figure 11.

Herbae annuae, 18–55 cm altae. Caules erecti, simplices vel ramosi, internodiis 3–12.5 cm longis, rubri-virides, pilosi trichomatibus multicellulosis usque 2 mm longis. Folia petiolis 0.1–2 cm longis, rubris; laminae anguste ovatae, 1.8–4.3 cm longae, 0.8–2.3 cm latae, pilosae utrinque, apice acuto vel aliquantum attenuato, basi rotundata vel cuneata; margines serrati vel serrulati. Pedunculi 1–7.1 cm longi, pilosi trichomatibus multicellulosis adpressis et effusis, eglandulosis. Capitula 0.4–0.6 cm alta, 0.6–1.5 cm lata. Involucrum campanulatum; phyllaria exteriora 2–3 mm longa, 1–1.7 mm lata, glabra, marginibus scariosis; phyllaria interiora 3–3.7 mm longa, 2–2.5 mm lata, glabra, marginibus scariosis. Receptaculum 2.5 mm altum, 1.3 mm diametro. Paleae extimae anguste ovatae, 2–2.8 mm longae, 1–1.6 mm latae, apice acuto vel obtuso, junctae ad basim binatim ad phyllarium contiguum; paleae interiores lanceolatae, attenuatae, 1.7–2.5 mm longae, 0.3–0.7 mm latae,

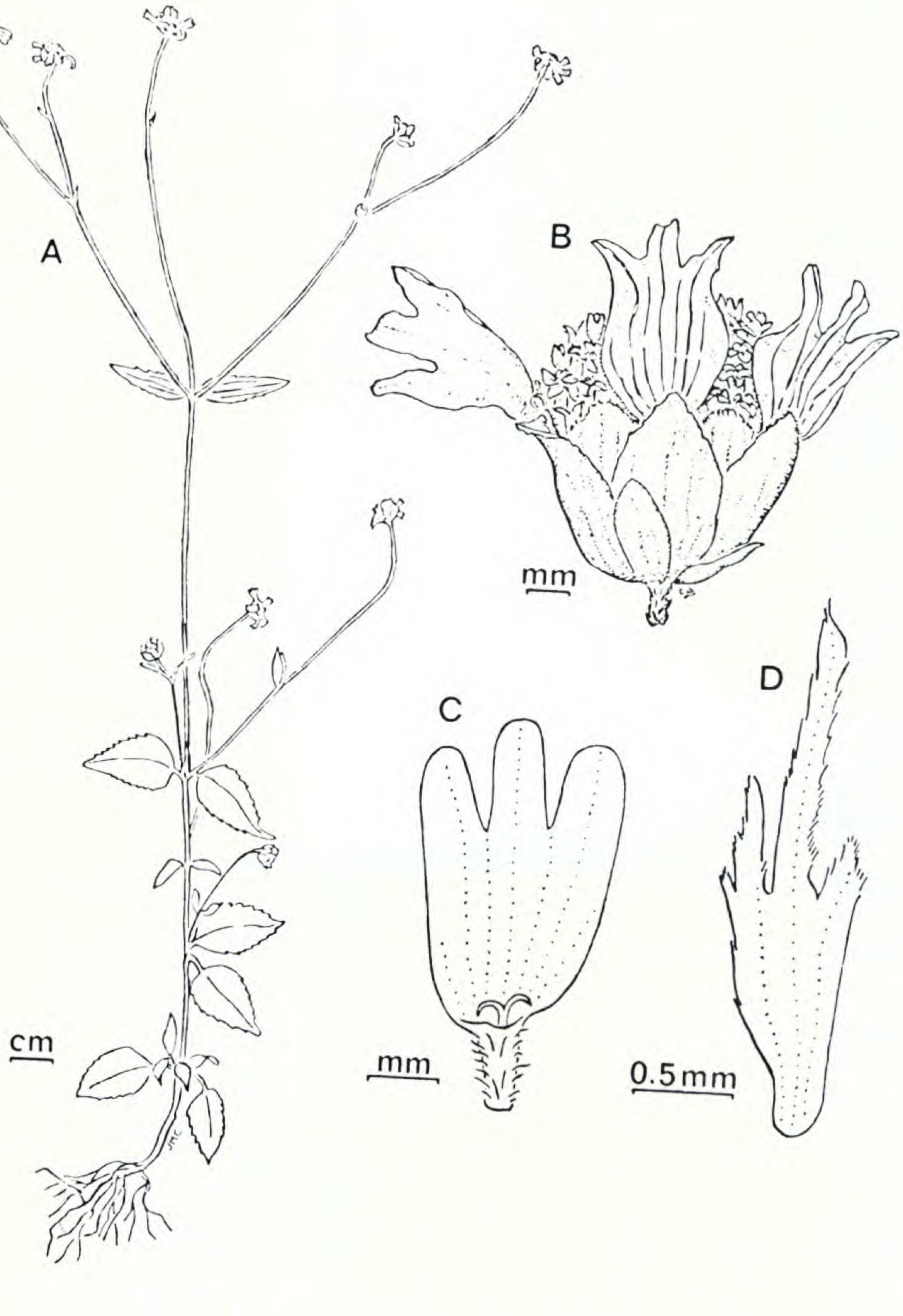

Figure 11. **Galinsoga longipes.** A, habit; B, head; C, ray corolla; D, inner pale. All *Cronquist 10308;* A and B (DUKE), C and D (US).

integrae vel aliquot lobo laterali acuto. Flosculi radii 5, corollis albis, venis purpureis; ligulae 2.5–6 mm longae, 2–3.5 mm latae, sparse brevipilosae in venis dorsalibus, lobis 3; tubi 1.5 mm longi; achenia 1.3 mm longa, 0.5 mm lata, glabra, epapposa. Flosculi disci 35–100, corollis luteis; fauces 1.3–1.5 mm longae, 0.7–1 mm diametro, lobis 0.4 mm longis, acutis; tubi 0.4–0.6 mm longi; antherae brunneolae, 0.8 mm longae, appendice ovata; achenia 0.8–1 mm longa, 0.4 mm lata, glabra, epapposa vel strigosa et pappi squamellae ca 20 inequales obovatae, laciniatae, obtusae vel 3–5 squamellis aristatis interspersis. Chromosomatum numerus ignotus.

TYPE: **Mexico:** Michoacán, ca 23 mi E of Morelia, 9 Oct 1965, *A. Cronquist 10308* (Holotype, NY!; isotypes, CAS! DUKE! ENCB! MEXU! MICH! MSC! TEX! US! WIS!).

DISTRIBUTION. Restricted to the pine-oak woodlands of the mountains of west-central Mexico (Figure 10), 1600–2440 m. Flowering from September to February.

Although distinguished by differences in peduncle and achene pubescence, ray corolla number and shape, and pale shape, *Galinsoga longipes* most closely resembles *G. triradiata.* Plants of *Anderson & Laskowski 4373* particularly bear a strong vegetative likeness to *G. triradiata.* Representatives of both species possess the tall stature and elongate internodes for which *G. longipes* was named. Similarly, both taxa are characterized by a few-headed capitulescence with heads on elongate peduncles and by compact involucres greatly exceeded in length by the ray ligules.

The elongate internodes and peduncles, and the few-headed capitulescence are features shared with species in sects. *Stenocarpha* and *Elata. Galinsoga longipes* and *G. triradiata* are placed in sect. *Galinsoga,* however, because they have small heads with small florets, usually less than 70 disc florets and five or fewer ray florets, and representatives of both species are known to flower when only a few centimeters tall.

SPECIMENS EXAMINED. **Mexico.** GUERRERO: 32–40 km W of Chilpancingo, near Omiltemi, *Anderson & Laskowski 4373* (MICH); Pilas, *Hinton et al. 10471* (ENCB, LL, MICH, US); El Voladerito, cerca de Coxtlahuacán, *Rzedowski 30273* (ENCB). MEXICO: local of Rincón, *Hinton 2431* (BM, F, GH, NY, US). MORELOS: Cempoala, *Lyonnet 802* (US).

7. **Galinsoga triradiata** Canne, sp. nov. Figure 12.

Herbae annuae, usque ad 75 cm altae. Caules erecti, internodiis usque 13 cm longis, virides-rubri, pilosi; trichomata multicellulosa effusa usque ad 2 mm longa trichomatibus immixtis glandulosis capitatis. Folia subsessilia vel petiolis 0.2–1 cm longis; laminae ovatae, 1.5–6.5 cm longae, 0.6–2.5 cm latae, pilosae utrinque, apice acuto, basi cuneata vel rotundata; margines serrati. Pedunculi 0.5–6 cm longi. Capitula 0.4–0.6 cm alta, 0.6–1.3 cm lata. Involucrum biseriatum, campanulatum; phyllaria exteriora 4, anguste triangulata-ovata, 1.2–1.8 mm longa, 0.7–1 mm lata, glandulosa pilosa, apice acuto, marginibus scariosis et minute laciniatis; phyllaria interiora ovata, convexa, 2.8–3.3 mm longa, 1.8–2 mm lata, glandulosa pilosa, marginibus scariosis. Receptaculum 1.4–1.8 mm alta, 0.9–1 mm diametro. Paleae extimae ovatae, junctae ad basim terni ad phyllarium contiguum, 2 mm longae, 1 mm latae; paleae interiores lineares vel anguste oblanceolatae, 2–2.3 mm longae, 0.3–0.5 mm latae, apice obtuso, aliquando rubro, marginibus subtiliter laciniatis. Flosculi radii 3–4 (–5), corollis albis, aliquando dorsaliter purpureis; ligulae obovatae, 3.5–6 mm longae, 4–7 mm latae, pilosae in venis dorsalibus, lobis 3, ca 1/2 ligulae longitudinis, obtusis; tubi 0.6–0.8 mm longi; achenia 1–1.4 mm longa, 0.5–0.6 mm diametro, glabra vel trichomatibus brevibus obtusis 4-cellularibus, epapposa. Flosculi disci 25–35, corollis luteis; fauces 1–1.5 mm longae, 0.8–1 mm diametro, lobis 0.3–0.4 mm longis; tubi 0.3–0.5 mm longi; antherae brunneolae, 0.6–0.8 mm longae, appendice ovata; achenia acheniis radiorum similia. Chromosomatum numerus ignotus.

TYPE: **Mexico:** Michoacán, northwestern foothills of Cerro Tancítaro, 13–14 km S of Peribán de Ramos, 1650–1700 m, 29 Nov 1970, *R. McVaugh 24828* (Holotype, MICH!; isotypes, DUKE! ENCB! LL! NY!).

DISTRIBUTION. Known from the pine-oak forests in the mountains of Michoacán, Mexico (Figure 10) where the species occurs in locally abundant colonies, 1100–1700 m. Flowering in October and November.

The specific epithet, *triradiata,* was chosen to emphasize the characteristic three-rayed condition of the heads. This species is

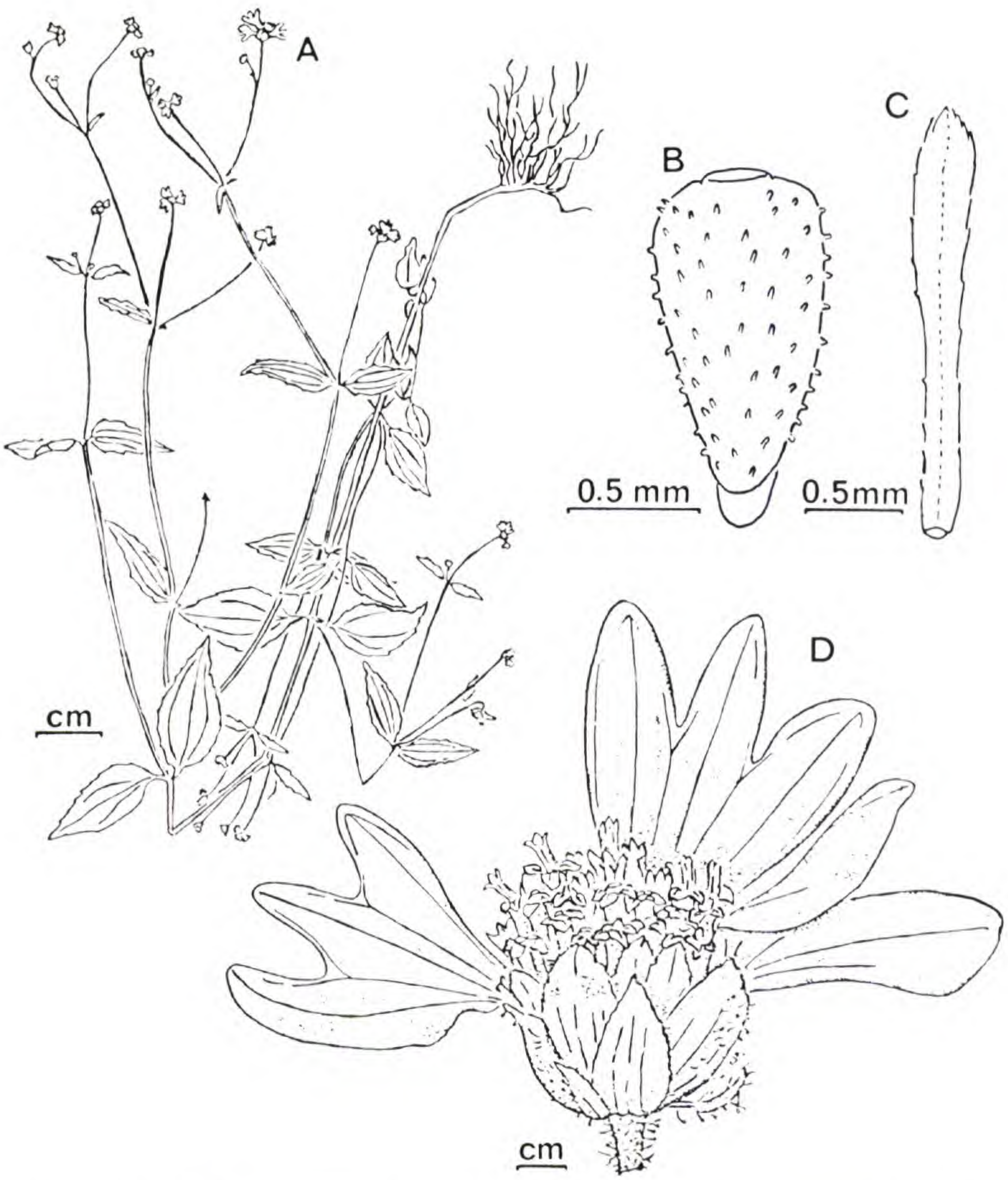

Figure 12. **Galinsoga triradiata.** A, habit; B, disc achene; C, inner pale; D, head. A and D, *McVaugh 24828* (NY); B and C, *Hinton et al. 15619* (MICH).

sharply defined from others by ray corolla and pale shape, and achene pubescence. Features discussed under *Galinsoga longipes* relate this taxon to *G. triradiata* as its closest relative. A discussion of sectional disposition of these species is also provided under *G. longipes*.

SPECIMENS EXAMINED: **Mexico.** MICHOACÁN: 5 km S of Ario de Rosales, *Ripley & Barneby 14824* (NY); 13 mi S of Ario de Rosales, *Cronquist 9733* (GH, MEXU, MICH, MO, MSC, NY, TEX, US); Tancítaro, *Hinton et al. 15619* (ENCB, LL, MICH, MO, US); 28 km SW of Arteaga, *Rzedowski 26623* (CAS, ENCB, MICH).

8. **Galinsoga caligensis** Canne, sp. nov. Figure 13.

Herbae annuae, 3–40 cm altae. Caules erecti vel decumbentes, rubri, glabri vel sparse pilosi prope basin usque moderate vel dense pilosi in ramis superis trichomatibus adpressis et effusis usque ad 1 mm longis. Folia petiolis 1–7 (–10) mm longis; laminae ovatae vel lanceolatae-ovatae, 1.5–4 (–6) cm longae, 0.4–2.5 cm latae, pilosae utrinque apice acuto, basi rotundata; margines ciliati, integri vel serrati. Pedunculi 0.8–5 cm longi. Capitula 5–6 (–9) mm alta, 8–10 mm lata. Involucrum biseriatum, campanulatum; phyllaria exteriora 2, ovata vel lanceolata-ovata, 2–3 (–3.8) mm longa, 0.6–1.5 mm lata, marginibus minute laciniatis et scariosis, glabris vel sparse pilosis; phyllaria interiora 5, ovata, 3–4.5 mm longa, 1.7–2.5 mm lata, glabra, aliquando purpurascentia, marginibus minute laciniatis et scariosis. Receptaculum 1.5–1.8 mm altum, 1.5 mm diametro. Paleae extimae ovatae-lanceolatae, 3.5–4 mm longae, 1–1.5 mm latae, junctae ad basim binatim ad phyllarium contiguum; paleae interiores lanceolatae, 2–3.8 mm longae, 0.5–1.2 mm latae, integrae vel aliquanto trifidae. Flosculi radii 5–8, corollis albis; ligulae 2–3.8 mm longae, 1.6–3 mm latae, lobis 3(–4); tubi 0.8–1.9 mm longi; achenia obconica, 1.4–1.7 mm longa, 0.5–0.6 mm diametro, glabra, epapposa. Flosculi disci 35–75; fauces 1.2–1.6 mm longae, 1 mm diametro, minute pilosae, lobis 0.4 mm longis; tubi 0.5–0.7 mm longi; antherae brunneolae, 1 mm longae, ad staminodia reductae vel absentes in seriem extremam flosculorum discorum, appendice ovata-oblonga; achenia anguste obconica, 1–1.3 mm longa, 0.4–0.6 mm diametro, glabra vel strigosa; pappi absentes vel squamellae lanceolatae, laciniatae, aristatae, 1.2–2 mm longae. Chromosomatum numerus ignotus.

TYPE: **Peru:** Lima, Dist. Pachacamac, Atacongo, among rocks in arid valley, 180 m, 14 Oct 1935, *Y. Mexia 4045* (Holotype, UC!; isotypes, GH! MO! US!).

DISTRIBUTION. Common to abundant among the rocks along the bases and slopes of the desert hills of coastal Peru (Figure 16), 70–600 m. Flowering from late July to November.

Galinsoga caligensis is endemic to the coastal desert region of western Peru. There, local dense fogs accumulate over the hills and dunes during the late winter months, August to October, saturating the air and soil with moisture. These areas, called lomas,

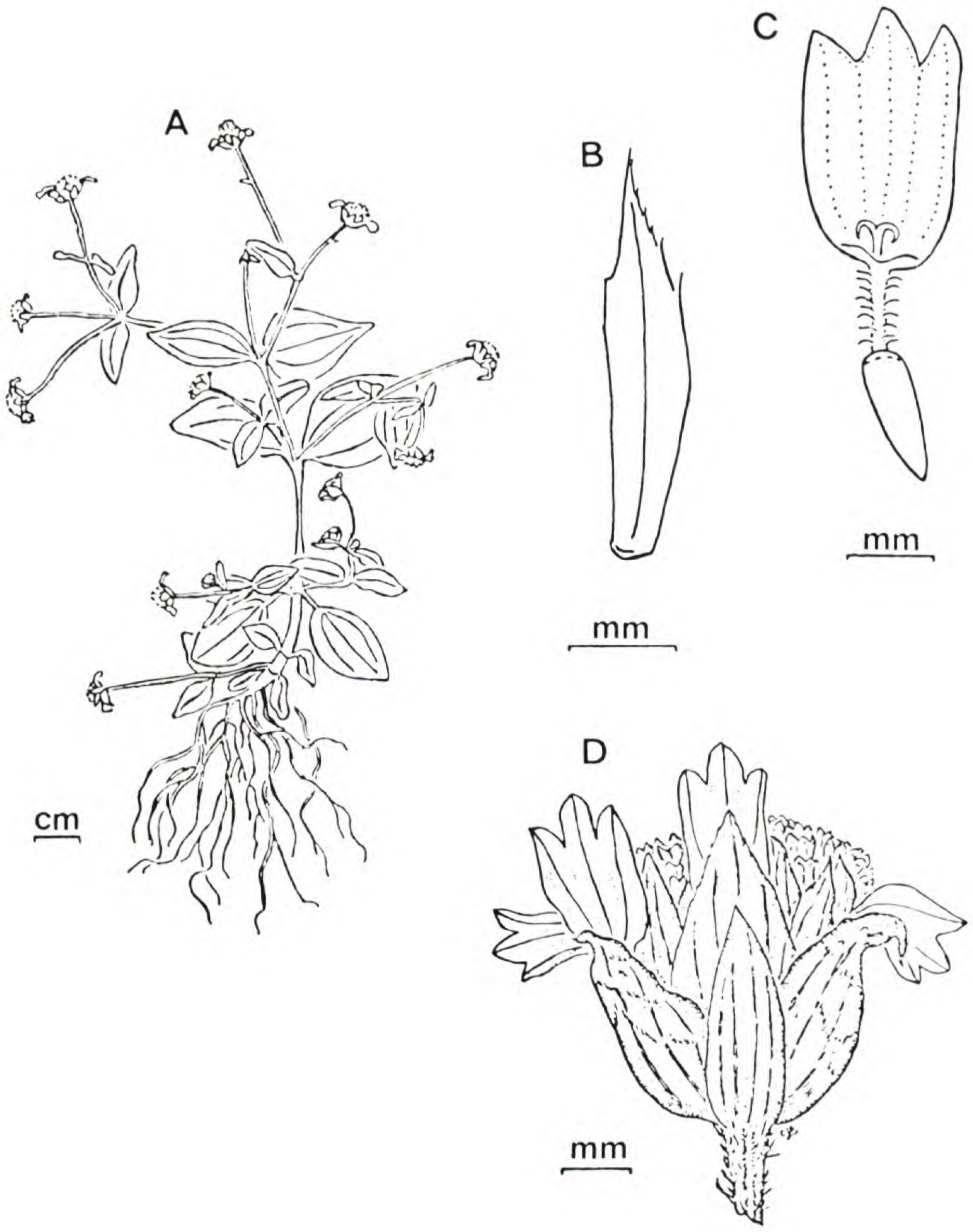

Figure 13. **Galinsoga caligensis.** A, habit; B, inner pale; C, ray floret; D, head. A and D, *Ferreyra 9534* (F); B and C, *Macbride 5952* (F).

support an interesting flora (Weberbauer, 1945) including this new species. The specific epithet, *caligensis,* was chosen because the taxon is known only from the foggy lomas.

One collection (*Vargas 4690*) is different from the others. None of the specimens in this collection contains a complete plant, but the branch on one of the sheets is 41 cm long, indicative of a plant far larger than others known to the species. The leaves are more narrowly elongate with sharply serrate margins and the phyllaries more attenuate. Because only one collection is known and especially because the principal differences are vegetative, I have not recognized the *Vargas 4690* collection at a formal taxonomic rank.

Galinsoga caligensis shows no obvious strong relationship to other Galinsogas. The rather long peduncles and the open capitulescence are unlike those of other South American species. The pappus, inner pales and ray ligules are like those of *G. quadriradiata,* but in other respects the two species differ.

SPECIMENS EXAMINED. **Peru.** LIMA: parte alta de Atocongo, *Cerrate 2388* (OS, USM); lomas de Atocongo, 32 km S of Lima, *Cerrate 2738, 2771* (OS, USM); lomas de Quilmana entre Mala y Cañete, *Ferreyra 223,* (OS, USM); *Ferreyra 6323* (US); lomas de Lurin, *Ferreyra 9534* (OS, USM); lomas de Doña Maria, *Ferreyra, Cerrate, & Tovar 16571* (OS, USM); lomas de Atocongo, *Grant 7499* (F, NY, US); Lurin, *Machride 5952* (F, US); lomas de Lachay, *Ochoa 598* (F, GH); lomas de Atocongo, *Stork, Horton, & Vargas 9291* (GH, UC); Lachay, near Chancay, *Tovar 378* (OS, USM); lomas de Lachay, *Vargas 4690* (CAS, F); hills of Asia, *Vargas 9305* (GH, UC).

9. **Galinsoga quadriradiata** Ruiz & Pavon, Syst. Veg. **1:** 198. 1798. TYPE: **Peru:** Lima, Lima and Chancay, 6 Jul-10 Aug 1781, *H. Ruiz & J. A. Pavon s.n.* (Holotype, MA; photograph of holotype, OS!; probable isotype, P!).

Galinsoga parviflora Cav. subsp.[here designated] *quadriradiata* (Ruiz & Pavon) Pers. Syn. Pl. **2:** 472. 1807. For a discussion of the uncertain status of Persoon's infraspecific taxa see Boivin (1962) and Chater & Brummitt (1966).

Galinsoga parviflora Cav. var. *quadriradiata* (Ruiz & Pavon) Poiret in Lamarck, Encyc. Meth. Supp. **2**(2): 701. 1812.

Galinsoga parviflora Cav. var. *discoidea* Ascherson & Garcke, Fl. Brandenberg **1:** 314. 1860, *pro syn.*

Galinsoga parviflora Cav. f. *discoidea* (Ascherson & Garcke) Thell. Allg. Bot. Z. Syst. **21:** 6. 1916.

Wilborgia urticaefolia HBK. Nov. Gen. Sp. Pl. **4:** 257. *t. 389.* 1818. TYPE: **Ecuador:** "Crescit juxta villam Marchionis de Miraflores, inter Mulalo et Pansache, alt. 1700 hex. (Regno Quitensi.)," Jun 1802, *F. H. A. von Humboldt & A. J. Bonpland 3055* (Holotype, P; photographs of holotype, F! GH! US!).

Jaegeria urticaefolia (HBK.) Spreng. Syst. Veg. **3:** 590. 1826.

Sabazia urticaefolia (HBK.) DC. Prodr. **5:** 497. 1836.
Baziasa urticaefolia (HBK.) Steud. Nomencl. Bot. **1:** 192. 1840.
Galinsoga urticaefolia (HBK.) Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn p. 102. 1852.
Stemmatella urticifolia (HBK.) O. Hoffm. ex Hieron., Bot. Jahrb. Syst. **28:** 603. 1901.
Vargasia caracasana DC. Prodr. **5:** 676. 1836. TYPE: **Venzuela:** Caracas, 1830, *M. Vargas 267* (Holotype, G-DC; photograph of holotype, US!; isotype, P!).
Galinsoga parviflora Cav. var. *caracasana* (DC.) A. Gray, Smithsonian Contr. Knowl. **5:** 98. 1853.
Galinsoga caracasana (DC.) Sch.-Bip. Bull. Soc. Bot. France **12:** 80. 1865.
Galinsoga quadriradiata Ruiz & Pavon var. *quadriradiata* f. *vargasiana* Thell. Allg. Bot. Z. Syst. **21:** 14. 1916. Based on type of *Vargasia caracasana* DC.
Galinsoga quadriradiata Ruiz & Pavon var. *hispida* (DC.) Thell. f. *vargasiana* (Thell.) Mosseray ex Brenan, Bot. Soc. Exch. Club Brit. Isles **12:** 94. 1939.
Galinsoga ciliata (Raf.) S. F. Blake f. *vargasiana* (Thell.) Lousley, Watsonia **1:** 240. 1950.
Adventina ciliata Raf. New Fl. N. Am. **1:** 67. 1836. TYPE: unknown, not at PH.
Galinsoga ciliata (Raf.) S. F. Blake, Rhodora **24:** 35. 1922. Combined incorrectly as *Galinsoga cilata* (Raf.) Blake.
Galinsoga parviflora Cav. γ *hispida* DC. Prodr. **5:** 677. 1836. TYPE: **Mexico:** "in Mexico circa urbem," 1 Aug 1827, *J. L. Berlandier 615* (Lectotype, P!; isolectotype, G-DC).
Galinsoga hispida (DC.) Hieron. Notizbl. Konigl. Bot. Gart. Berlin **19:** 15. 1907, *non* Benth. 1845. *nom. illegit.*
Galinsoga quadriradiata Ruiz & Pavon var. *hispida* (DC.) Thell. Allg. Bot. Z. Syst. **21:** 11. 1916.
Galinsoga aristulata Bicknell, Bull. Torrey Bot. Club **43:** 270. 1916. Based on the type of *G. parviflora* Cav. var. *hispida* DC. The new specific epithet was supplied by Bicknell due to the previous publication of *G. hispida* Benth.
Galinsoga hispida Benth. Bot. Voy. Sulph. 119. 1845. TYPE: **Ecuador:** Guayaquil, 1841, *R. B. Hinds s.n.* (Lectotype chosen, K!; photograph of lectotype, US!).
Galinsoga brachystephana Otto, Index Sem. Hort. Berol. 1840. *nom. nud.*
Viborgia brachystephana (Otto) Heynh. Nomencl. Bot. Hort. **2:** 707. 1846. *nom. illegit.*
Galinsoga brachystephana Otto ex Heer & Regel, Index Semin. Hort. Turic, anno 1846 coll. 1847. TYPE: "Hort. Berol." *s.d. E. Regel s.n.* (Probable holotype, ZT!).
Galinsoga hispida Benth. var. *purpurascens* Fenzl. Del. Sem. Hort. Vindob. Advers. Bot. Stirp. e Sem. 1849 et 1850. p. 2. 1851. *nom. superfl.* Published as a new name for *Galinsoga brachystephana* Otto ex Heer & Regel but treated as a variety of *G. hispida* Benth.

Galinsoga quadriradiata Ruiz & Pavon var. *quadriradiata* f. *purpurascens* (Fenzl) Thell. Allg. Bot. Z. Syst. **21:** 15. 1916.

Galinsoga hispida Benth. var. *albiflora* Fenzl. Del. Sem. Hort. Vindob. Advers. Bot. Stirp. e Sem. 1849 et 1850. p. 2. 1851. *nom. nud.*

Galinsoga quadriradiata Ruiz & Pavon var. *quadriradiata* f. *albiflora* Fenzl ex Thell. Allg. Bot. Z. Syst. **21:** 15. 1916. TYPE: **Costa Rica:** "prope San Jose ad fossam in campis sabanas dictis," 5 Jun 1875, *H. Polakowsky 1* (in part), (Lectotype chosen, BM!). Thellung's description of the taxon was quoted from a description by G. Hieronymus (1901). The type at BM contains a specimen of *G. quadriradiata* and a fragment of *Jaegeria hirta* (Lag.) Less.

Galinsoga humboldtii Hieron. Bot. Jahrb. Syst. **28:** 618. 1901. TYPE: Locality and date not indicated, *F. H. A. von Humboldt & A. J. Bonpland s.n.* (Holotype, B, destroyed; photographs of holotype, NY! US!, fragment of type, US!).

Stemmatella lehmannii Hieron. Bot. Jahrb. Syst. **28:** 602. 1901. TYPE: **Colombia:** Cauca, vicinity of Popayán, *s.d. F. C. Lehmann 5667* (Holotype, B, destroyed; fragment of type, US!).

Stemmatella urticifolia (HBK.) O. Hoffm. ex Hieron. var. *eglandulosa* Hieron. Bot. Jahrb. Syst. **36:** 487. 1905. TYPE: **Peru:** near Cutervo, Apr 1879, *Jelski 609* (Holotype, B?).

Galinsoga bicolorata St. John & White, Rhodora **22:** 99. 1920. TYPE: **Mexico:** Chiapas, near Tumbala, 4000–5500 ft., 20 Oct 1895, *E. W. Nelson 3356* (Holotype, GH! isotype, US!).

Sabazia urticaefolia (HBK.) DC. var. *venezuelensis* Steyerm. Fieldiana, Bot. **28:** 672. 1953. TYPE: **Venezuela:** Lara, slopes of mountain between Santo Domingo and Los Quebraditos, south of Las Sabanetas, above Humocaro Bajo, 8 Feb 1944, *J. A. Steyermark 55379* (Holotype, F; isotype, US!).

Galinsoga eligulata Cuatr. Revista Acad. Colomb. Ci. Exact. **9:** 241. 1954. TYPE: Columbia: Caldas, Chinchiná, "Centro Nacional de Investigaciones del Café" 22 Nov 1946, *J. Cuatrecasas 23098* (Holotype, F! photograph, US!).

Ageratum perplexans M. F. Johnson, Ann. Missouri Bot. Gard. **58:** 80. 1971. TYPE: **Bolivia:** Yungas, 1890, *A. Miguel Bang 235* (Holotype, MICH!; isotypes, GH! MO! MSC! NY! US! WIS!). The sheets at GH, MSC, and WIS contain specimens of *Galinsoga parviflora* Cav. as well as *G. quadriradiata* Ruiz & Pavon.

Galinsoga × *Plikeri* Giacomini, Atti Ist. Bot. Univ. Pavia **9:** 186. 1950. TYPE: unknown. *nom. illegit.* Published as a hybrid of *G. ciliata* (Raf.) S. F. Blake and *G. parviflora* Cav. without Latin diagnosis or designation of type. The Italian description is that of *G. quadriradiata.*

Annual herbs to 62 cm tall. Stems erect or spreading, sparsely pilose below to densely strigose and pilose above with multicellular trichomes, often with red, glandular capitate trichomes intermixed on the younger branches and peduncles. Leaves with petioles 0.2–6 cm long; blades broadly to narrowly ovate, 1.6–9.5 cm long, 0.5–5.5 cm wide, at the apex acute to obtuse, at the base cuneate to rounded, with both surfaces sparsely to densely pilose; margins ciliate, serrulate to coarsely serrate, or crenate-serrate. Peduncles

0.2–5.2 cm long. Heads 3–8 mm tall, 2.1–10 mm wide. Involucre campanulate to cylindro-campanulate, glabrous or with scattered glandular capitate trichomes; outer phyllaries 1–3, unequal, narrowly to broadly ovate or lanceolate, 0.9–3 mm long, 0.5–2.2 mm wide, with the margins entire to minutely laciniate; inner phyllaries ovate, 2.5–4 mm long, 1.5–2.7 mm wide, with the margins minutely laciniate and scarious above the middle. Receptacle 0.8–2.3 mm tall, 1–2.5 mm diam. Outer pales broadly elliptic to obovate, 2–3 mm long, 0.6–1.8 mm wide, joined in groups of 2 or 3 at the base to an adjacent phyllary; inner pales lanceolate to oblanceolate, 1.8–3.3 mm long, 0.4–1 mm wide, entire to shallowly and irregularly trifid. Ray florets 5, rarely 4 or 8, with the corollas white to reddish-purple, or white with reddish veins; ligules 0.9–2.8 mm long; 0.7–2.5 mm wide, or rarely absent, obovate to quadrate, occasionally bilabiate with 1 or 2 oblong inner lobelets to 1.2 mm long; tubes 0.5–1.2 mm long; achenes 1.3–1.8 mm long, 0.5–0.8 mm diam, glabrous or strigose, epappose or with the pappus coroniform, of a few bristles, or 8–20 elliptic to obovate, fimbriate, often aristate, white scales, 0.2–1.4 mm long. Disc florets 15–65, corollas sometimes with reddish-purple lobes and throats, throats 0.8–1.5 mm long, 0.4–0.7 mm diam; tubes 0.3–0.5 mm long; anthers 0.5–0.7 mm long with the appendage ovate; achenes somewhat angular, 1.1–1.6 mm long, 0.5–0.8 mm diam, strigose, epappose or with a pappus of a few narrow, fimbriate scales or usually 20, lanceolate or somewhat oblanceolate, fimbriate, usually aristate scales to 1.5 mm long. Chromosome numbers, n = 16, 24, 32.

DISTRIBUTION. Apparently native to central Mexico, but now weedy in most temperate and subtropical areas of the New World and Europe. The species is found also in parts of Nepal, Japan, the Philippines, and Africa (Figure 14), 150–3270 m. Flowering the year round or until the first killing frost.

Galinsoga quadriradiata is the most morphologically variable species in the genus. This variability may be due to several causes. Presumably, the taxon underwent initial divergence and speciation in the mountainous areas of Mexico where populations experienced considerable geographical isolation and subsequently developed reproductive isolation to varying degrees. This resulted in the formation of rather discreet morphological units. The development of self-fertility in *G. quadriradiata* (known to occur now;

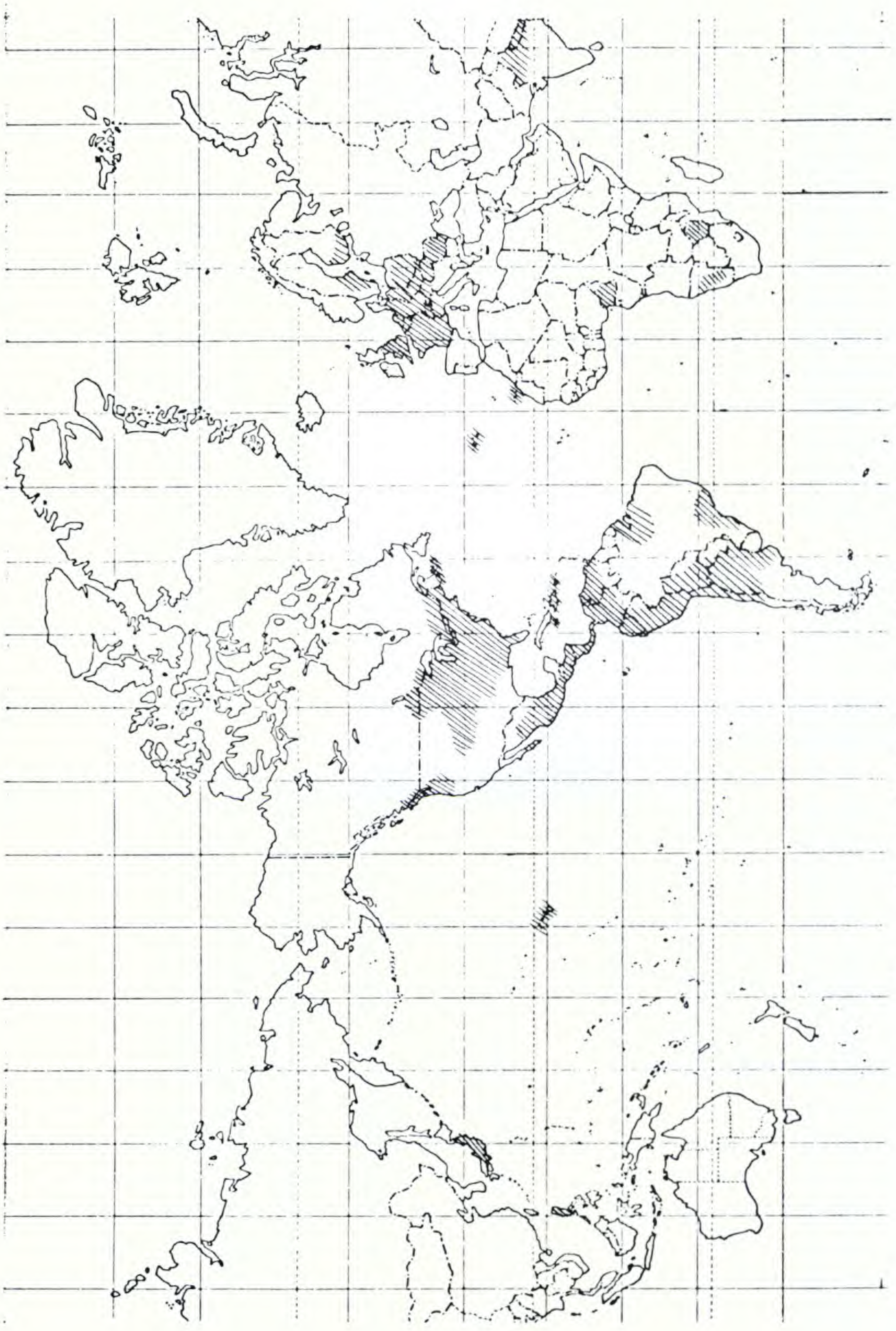

Figure 14. **World distribution of Galinsoga quadriradiata.**

Canne, unpubl.) undoubtedly enhanced the taxon's ability to colonize new locals. Also, plants of *G. quadriradiata* can flower when very young (e.g., when only a few centimeters tall) and continue to do so throughout the growing season. The large number of heads per plant in continuous production throughout the growing season represents an enormous reproductive potential.

A mosaic of populational variability probably formed as early colonization continued. Eventually, however, through natural and later, man-influenced disturbances, formerly isolated variants came into contact and hybridization occurred across weakly formed reproductive barriers. The advent of agriculture and road building must have significantly aided colonization of this now weedy, morphologically plastic, and genetically heterogeneous taxon.

In its native areas of the New World, two morphological variants of *Galinsoga quadriradiata* can be distinguished, although both are internally variable. The first variant, which extends from northern South America through the United States into Canada, tends to have a short conic receptacle, entire inner pales, glandular capitate trichomes, and peduncles to about 2 cm long. The second variant ranges from Durango, Mexico south through Central America into Colombia, and in its purest form has a tall conic receptacle, shallowly and irregularly trifid pales, aglandular trichomes and peduncles 2–3.5 cm long.

The two variants occur sympatrically in Mexico and Central America, and at least some plants in 50% of the populations from which I collected in Mexico and Guatemala were clearly intermediate in morphology. Pollen from the intermediate plants (in lactophenol cotton blue) showed a range of stainability from 36%–98%. Microsporocytes routinely had meiotic irregularities including multivalent formation, anaphase bridges and fragments, and lagging chromosomes (Figure 6). The presence of two and three anaphase bridges and fragments of differing sizes may indicate that some of the Mexican and Guatemalan intermediate plants are heterozygous for at least two chromosomal inversions. The range of morphological intergradation, pollen viabilities, and meiotic irregularities suggest that the intermediate plants probably are to some extent F_1 hybrids, but also later generation hybrids and backcrosses.

The morphological variability of *Galinsoga quadriradiata* is further complicated by a pink to red-rayed variant which occurs

from Chiapas, Mexico, into South America. The Mexican and Central American members of this form are known to be tetraploid at $n = 16$. Specimens collected in Peru were uniformly hexaploid at $n = 24$ except for one population at $n = 32$.

Morphologically the pink-rayed variant is similar to other plants of *Galinsoga quadriradiata*, but it tends to have coarsely crennate-serrate leaves, cylindro-campanulate involucres, and ray ligules which project at right angles from the head. Accurate identification of this form is made difficult because the involucre shape, and particularly the ligule position, are obscured when the plants are pressed. Ray corolla color varies from white to deep reddish-purple in living plants and in some cases the white or pink color changes to dark red when plants are pressed and dried.

Definition of the variant is clouded by extensive intergradation with both of the white-rayed variants in southern Mexico, Central America and northern South America where all three morphic types occur as weeds. The mode of origin of the higher polyploid levels ($n = 24$ & 32) is unknown, but the Peruvian plants at the higher ploidy levels are the most distinctive members of this rather weakly defined pink-rayed group.

The lengthy synonymy for *Galinsoga quadriradiata* is certainly a reflection of the taxon's morphological variability. No infraspecific taxa are presently recognized due to the extensive intergradation among the variants discussed here. There is little geographical separation of the morphic forms other than white-rayed members tend to be mostly North American and pink-rayed members tend to be mostly South American. This trend by itself is not only unworthy of formal recognition but is valid only for the New World. Dispersal of *G. quadriradiata* to the Caribbean Islands and the Old World (Figure 14) has thoroughly intermixed the three variants in these regions.

One case of intergeneric hybridization involving *Galinsoga quadriradiata* is suspected from herbarium material. Collections made in Chiapas, Mexico (*Ton 982, 1263, 1277*) are morphologically intermediate between *G. quadriradiata* and *Sabazia sarmentosa* Less. var. *sarmentosa*. *Galinsoga quadriradiata* and *Sabazia sarmentosa* differ in quantitative features of the heads but also in that *S. sarmentosa* is perennial with stems arising from a caudex while *G. quadriradiata* is an annual lacking a caudex. *Sabazia sarmentosa* is characterized by reddish brown anthers and usually has

larger heads on long peduncles. *Galinsoga quadriradiata,* on the other hand, has yellow anthers and small heads on short peduncles. The leaves, involucres, pales, achenes, and pappus scales of the two species are similar.

The putative hybrids have the decumbent, weak stems and peduncle length of *Sabazia sarmentosa* but head size and clustering more characteristic of *Galinsoga.* Pollen from the putative hybrids is of varying sizes and many of the grains are misshapen. No pollen at all was found in anthers inspected from *Ton 1263* (MO). No mature achenes were seen on any of the plants. Longpre (1970) reported the chromosome number of *S. sarmentosa* var. *sarmentosa* as $n = 24$. *Galinsoga quadriradiata* from Chiapas has been counted as n = ca 16 (Turner, Powell, & King, 1962). The difference in polyploid levels as well as genetic differences undoubtedly account for the apparent sterility of the hybrids.

Galinsoga quadriradiata is also implicated in an interspecific hybridization with *G. subdiscoidea.* Details of this situation are discussed under the latter species.

REPRESENTATIVE SPECIMENS:[1] **Canada.** BRITISH COLUMBIA. New Westminster Dist.: Vancouver, *Bird 178* (BM). ONTARIO. Manitoulin Dist.: Gore Bay, *Montgomery & Shumovich 1258* (OAC). **Costa Rica.** CARTAGO: Cartago, *Stork 1064* (F, GH, US). **Dominican Republic.** Sapotén, *Liogier 15051* (NY). **El Salvador.** CHALATENANGO: Los Esesmiles, *Tucker 1039* (F, LL, MICH, NY, UC, US). **Guatemala.** CHIMALTENANGO: Chimaltenango, *C 35*;* 4 km E of Chimaltenango, *C 46*;* 9.3 km SE of Patzun, *C 47*;* 10 km W of Patzun, *C 48*.* ESCUINTLA: 2 km N of Palin, *C 30*.* GUATEMALA: Guatemala City Airport, *C 31*;* 22.4 km W of Guatemala City Airport, *C 32*;* Lake Amatilan, *C 37*, C 38*;* 6 km S of Villa Nueva, *C 40*.* SACATEPEQUEZ: ca 5 km W of Guatemala-Sacatepequez boundary, *C 28*;* 6.2 km SE of Antigua, *C 29*;* 5.5–6.6 km SW of jct rd. to Antigua and Rte. CA1, *C 33*, C 34*;* 7 km S of Antigua, *C 44*.* SOLOLA: 19.2 km W of Patzun, *C 50*;* 8.8 km W of San Lucus of Toliman, *C 51*;* E of San Lucas, *C 52*.* **Honduras.** COMAYAGUA: vicinity of Siguatepeque, *Standley 56521* (F, US). **Mexico.** BAJA CALIFORNIA: the Laguna, *Jones 27758* (UC). CHIAPAS: San Cristobal las Casa, *Breedlove & Raven 13278* (DS, ENCB, LL, MICH, NY, US). CHIHUAHUA: Quicorichi, *Gentry 1935* (GH, MO, TEX, UC, US). COAHUILA: Saltillo, *Palmer 790* (BM, F, GH, MO, NY, US). DURANGO: 10.5–12.7 mi SW of La Ciudad, *KC 8872*, KC 8889*, KC 8890*;* 14 mi SW of La Ciudad, *KC 8943*;* GUERRERO: 0.3 mi N of Puente Huajgutla, *KC 9106*;* Taxco, *KC 9111*;* JALISCO: 1.2 mi NW of Magdalena Airport, *KC 9006*;* 25.8–27.5 mi SE of Magdalena Airport, *KC 9017–2*,* 4.9 mi SE of Arenal, *KC 9019*.* MEXICO: 3.2 mi N of Tenancingo,

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[1] *Canne* = *C*, *Canne & Hruschak* = *CH*, *Canne & Schunke* = *CS*, *Keil & Canne* = *KC*. Chromosome vouchers at OS are indicated by *($n = 16$), †($n = 24$) and §($n = 32$).

KC 9091;* 11.5 mi N of Ixtapan de la Sal, *KC 9092**. MICHOACAN: 11.4 mi N of Uren, *KC 9051-1*;* 17.2 mi E of Zamora, *KC 9054*;* 26.7 mi E of Zamora, *KC 9055*;* 2.6 mi E of La Vesca, *KC 9056*;* 4.4 mi W of jct rd. to Coeneo & Rte. 15, *KC 9057*;* 54 mi E of Zamora, *KC 9058*;* 1 mi E of Quiroga, *KC 9071*;* 10 mi E of Quiroga, *KC 9072*;* 14 mi E of Morelia, *KC 9076*;* 2.8 mi W of jct rd. to Zinapecuaro & Rte. 15, *KC 9077*;* 4.7 mi W of jct rd. to Los Azufres & Rte. 15, *KC 9078;* 0.8 mi E of jct Rte. 122 & Rte. 15, *KC 9079*;* 1.8 mi S of Tuxpan, *KC 9080*;* 3 mi E of Zitacuaro, *KC 9083*;* 12 mi E of Zitacuaro, *KC 9084**. MORELOS: Cuernavaca, *KC 9144*, KC 9145-2**. NAYARIT: La Atarjea, *Mexia 882* (BM, CAS, DS, GH, MO, NY, UC, US). PUEBLA: 22.7 mi E of Puebla-Mexico boundary, *KC 9170-2**. SAN LUIS POTOSI: Xilitla, *Rzedowski 10516* (ENCB). SINALOA: 1.2 mi E of Santa Lucia, *KC 8836*;* 3 mi E of Sta. Rita, *KC 8838**. VERACRUZ: 0.5 mi W of bridge between Cordoba & Orizaba, *KC 9179*;* 5.6 mi SE of Yanga, *KC 9180*;* SE of Jalapa Enriques, *KC 9186*;* ca 4 mi NW of Jalapa Enriques, *KC 9187*;* 5.4 mi E of road to Las Vigas on Rte. 140, *KC 9198*;* 2–12.6 mi E of Tezuitlan, *KC 9200*, KC 9201*, KC 9202**. **Nicaragua.** GRANADA: Volcan Mombacho, *Narvaez 3893* (NY, UC). . **Panama.** CHIRIQUI: Bajo Chorro, *Davidson 135* (F, GH, MO). **Puerto Rico.** Reserva Forestal de Toro Negro, *Stimson 1467* (DUKE, GH, MICH, UC, US). **United States.** ALABAMA: Mobile Co., Mobile, 10 Aug 1898, *Mohr s.n.* (US). ARKANSAS: St. Francis Co., Forest City, *McDaniel 1528* (NY). COLORADO: Boulder Co., Boulder, *Ewan & Ewan 14398* (TEX, UC, US). CONNECTICUT: Fairfield Co., Newtown, *Eames 201* (GH, MICH, MSC). FLORIDA: Leon Co., Tallahassee, 17 Jun 1926, *Harper s.n.* (NY, US). GEORGIA: Polk Co., Rockmart, *CH 105* (OS). HAWAII: Hawaii Co., Kilauea Volcano, *Fosberg 39311* (US). ILLINOIS: Cook Co., Chicago, *Gates 12548* (DS, TEX, US). INDIANA: Marion Co., Indianapolis, *Friesner 18115* (GH, NY, TEX, US). IOWA: Polk Co., Des Moines, *van Bruggen 2483* (US). KANSAS: Coffey Co., 7 mi N of Westphalia, *Magrath & Robinson 6764* (ENCB). KENTUCKY: Edmonson Co., Mammoth Cave, *CH 103**. Hart Co., jct Rte. US 31E & Ky 936, *CH 101*;*Horse Cave, *CH 102**. Jefferson Co., Louisville, *CH 97**. Nelson Co., New Haven, *CH 100**. Oldham Co., S. Oldham, *CH 96**. Simpson Co., Franklin, *CH 104**. Trimble Co., Bedford, *CH 95**. MAINE: Penobscot Co., Orono, *Gregory 508* (DS, NY). MARYLAND: Frederick Co., Thurmont, *CH 140*;* Emmitsburg, *CH 141-2**. MASSACHUSETTS: Middlesex Co., Winchester, *Smith, Schubert, & Rouleau 892* (ARIZ, CAS, DS, DUKE, FSU, GH, LL, MICH, MO, MSC, NY, UC, US, WIS). MICHIGAN: Washtenaw Co., Ann Arbor, *McVaugh 23636* (MICH). MINNESOTA: Cass Co., Leech Lake, *Stevens 2755* (UC, US). MISSOURI: Jackson Co. Kansas City, *Bush 8157* (GH, UC, US). NEBRASKA: Lancaster Co., Lincoln, *Kiener 16975* (GH). NEW HAMPSHIRE: Cheshire Co., 2 mi W of Jaffrey Center, *Gregory 503* (DS, NY). NEW JERSEY: Somerset Co., Watchung, *Moldenke 8908* (BM, MO, NY). NEW YORK: Cattaraugus Co., Machias, *CH 173*;* between Ellicottville & Great Valley, *CH 174**. Chemung Co., Reeds, *CH 164*;* Elmira, *CH 165*;* Livingston Co., Avon, *CH 170**. Monroe Co., Penfield, *CH 168*;* Henrietta, *CH 169*;* Schuyler Co., Watkins Glen, *CH 166**. Wyoming Co., Perry, *CH 171*;* Arcade, *CH 172**. Yates Co., Dresden, *CH 167**. NORTH CAROLINA: Buncombe Co., S of Asheville, *CH 121*;* 2 mi NW of Fairview, *CH 122*;* 10.6 mi SE of Fairview, *CH 123**. Burke Co., Morganton, *CH 126*;* N of Morganton, *CH 127**. Granville Co., Oxford, *CH 129**. Haywood Co., near Maggie, *CH 120**. Henderson Co., 3.8 mi N of N.C.-S.C. border, Rte. US 25, *CH 109*;* Hendersonville, *CH 110**. Iredell Co., 2 mi W of Statesville, *CH 128**.

Jackson Co., Cashiers, *CH 114**; Sylvia, *CH 117**; 1.6–3.7 mi S of Cherokee, *CH 118**, *CH 119**. Macon Co., Highlands, *CH 115**; N of Gneiss, *CH 116**. Rutherford Co., 11.1 mi SE jct US 74 with NC 9N, *CH 124**; 5 mi S of jct US 64 N & NC 226, *CH 125**. Transylvania Co., Penrose, *CH 111**; 10.9 mi SW of Penrose, *CH 112**; 2.6 mi E of jct US 64, *CH 155**. Northumberland Co., Dalmatia, *CH 153**, Sunbury, *CH 154**. Sullivan Co., Mildred, *CH 160**. Westmoreland Co., 2 mi E of jct US 119 & 22 with PA 981, *CH 187**; 11.4 mi W of jct US 119 & 22 with PA 981, *CH 188**. York Co., Thomasville, *CH 144**; Yorktown, *CH 145**. SOUTH CAROLINA: Grenville Co., 4.8 mi E of jct S.C. 414 and S.C. 253, *CH 107–1**; 3.3 mi N of jct US 25 & S.C. 414, *CH 108**. Spartanburg Co., Spartanburg, *CH 106**; Campobello, *CH 107–2**. VERMONT: Windham Co., Jamaica, *Moldenke 8712* (BM, MO, NY). VIRGINIA: Albemarle Co., 4.4 mi E of jct US 250 & Interstate 64, *CH 135**; Monticello, *CH 136**. Amherst Co., Clifford, *CH 131**. Campbell Co., Lychburg, *CH 130**. Loudon Co., Leesburg, *CH 139**. Orange Co., 4.7 mi SW of Orange, *CH 137**. WEST VIRGINIA: Barbour Co., 6.6 mi NW of jct W. VA. 76 & US 250, *CH 65**. Doddridge Co., 7.3 mi E of jct US 50 & W. VA. 18, *CH 62**. Fayette Co., 6.2 mi E of jct US 60 & US 19, *CH 76**; Lookout, *CH 77**. Greenbrier Co., White Sulfur Springs, *CH 73**; 4.6 mi W of Lewisburg, *CH 74**; Rupert, *CH 75**. Harrison Co., Salem College, *CH 64**. Kanawha Co., 8.7 mi NW of Charleston, *CH 79**. Pocahontas Co., 28 mi N of Frost, *CH 71**. Putnam Co., 0.6 mi S of jct W. VA. 62 & W. VA. 34, *CH 80**. Randolph Co., Elkins, *CH 68**; 10.5 mi S of Elkins, *CH 69**; 19.8 mi S of Elkins, *CH 70–1**. Richie Co., 0.3 mi S of jct US 50E & W. VA. 31, *CH 60**; Harrisville, *CH 61**. Wood Co., Parkersburg, *CH 59**. **Argentina.** JUJUY: Jujuy, *Everdam & Beetle 22413* (GH). **Bolivia.** COCHABAMBA: Incachaca, *Steinbach 5741*, (F, GH, MO, NY, US). **Brazil.** MINAS GERAIS: Vicosa, *Irwin 2035* (NY, TEX, UC, US). **Chile.** without locality, 1790, *Haenke s.n.* (F). **Colombia.** CUNDINAMARCA: 4 km WNW of Caqueza, *King & Guevara 5869* (F, NY, US). **Ecuador.** AZUAY: 14 km W of Cuenca, *King 6655* (US). **Peru.** CUZCO: Machu Picchu, *C 274*†, *C 276*†; Machu Picchu train station, *C277*†; *C278*†. HUANUCO: Tingo Maria, *C 217*†; *C 220*†; Fundo San Semond, *CS 197*†; *Chinchao, CS 200*†; Carpish Pass, *CS 201*§; *Chullqui, CS 203a*†; Cotosh, *CS 206*†; LaEsperanza, *CS 209a*†; Cueva de las Lechuzas, *CS 222*†; Rio Bella near Cueva de las Lechuzas, *CS 223*†. JUNIN: Santa Rosa de Ocopa, *CS 237*†; Oreja de Capelo, *CS 263*†, *CS 264*†. **Venezuela.** Distrito Federal, El Avila, *Williams & Alston 28* (BM, F, NY, US).

Austria. VIENNA: Wien, 1959, *Guglia s.n.* (CAS, FSU, WIS). **Belgium.** WEST FLANDERS: Wervik, 1939, *Desphmques s.n.* (MO, UC, US). **Czechoslovakia.** CENTRAL BOHEMIA: Pruhonice, *Devl 92* (NY, TEX, UC). **Denmark.** JUTLAND: Pinds Mole near Aarhus, *Nielsen & Pedersen 484* (DS). **Finland.** NYLANDI: Helsinki, 18 Aug 1960, *Erkamo s.n.* (UC). **France.** BASSES-PYRENEES: Bayonne, *Jallu 5534* (CAS). **Netherlands.** UTRECHT: Utrecht, *Leeuwenberg 394* (WIS). **Poland.** KRAKOW: Krakow, *Trzcinska 184* (MO, MSC, NY, UC). **Portugal.** AZORES: São Miguel, *Dolman 398* (BM). **Switzerland.** near Milchbuck, 27 Oct 1931, *Koch s.n.* (DS). **England.** SURREY: Kew, *Summerlayes 1286* (NY, TEX). **West Germany.** BAVARIA: Munich, 20 Aug 1929, *Ganz s.n.* (CAS). **Cameroon.** EAST CAMEROON: Wakwa, *Amshoff 457* (A). **Southwest Africa.** WINDHOEK: Windhoek, *Giess 233* (NY). **India.** UTTAR PRADESH: Dehra Dun, *Daval 2878* (US). **Japan.** TOKYO: Tokyo, 20 Oct 1952, *Suzuki s.n.* (UC). **Nepal.** Kathmandu, *Bhatt 113* (UC). **Philippines.** LUZON: Baguio, *Steiner 855* (US).

10. **Galinsoga boliviensis** Canne, sp. nov. Figure 15.

Herbae annuae, 7.5–14 cm altae. Caules erecti, ramosi, virides-rubri, pilosi. Folia petiolis 2–10 mm longis; laminae ovatae vel ovatae-lanceolatae, 1.3–4 cm longae, 0.5–1.8 cm latae, pilosae utrinque, apice acuto, basi rotundata; margines ciliati, integri vel remote serrulati. Pedunculi 0.1–1.3 cm longi. Capitula 4–5 mm alta, 4–7 mm lata. Involucrum campanulatum; phyllaria exteriora ovata-lanceolata, 2.5–3.6 mm longa, 1.2–2.8 mm lata, marginibus infra medium minute laciniatis et scariosis; phyllaria interiora ovata, usque 4.5 mm longa, glabra vel sparse pilosa, marginibus infra medium minute laciniatis et scariosis. Receptaculum 1.3 mm altum, 1.5 mm diametro. Paleae extimae ovatae-lanceolatae, 3–3.7 mm longae, 1–1.6 mm latae, junctae ad basim binatim ad phyllarium contiguum; paleae interiores lanceolatae, 3–3.3 mm longae, 0.8–1 mm latae, integrae vel aliquantum trifidae. Flosculi radii 5, corollis albis; ligulae 1.4–2.3 mm longae, 2 mm latae, lobis 2–3; tubi 0.8–1 mm longi; achenia obconica, 2–2.3 mm longa, 0.8 mm diametro, apice sparse strigosa, epapposa. Flosculi disci ca 26, corollis luteis; fauces 1.3 mm longae et 0.7 mm diametro, lobis 0.3–0.4 mm longis, acutis, papillosis; tubi 0.3–0.5 mm longi; antherae brunneolae, 0.7–0.8 mm longae, appendice oblonga, ca 1/3 antherae longitudinis; achenia subteretia, anguste obconica, 1.7–2 mm longa, 0.5 mm diametro, strigosa vel glabra; pappi absentes vel squamellae ca 15, inequales, lanceolatae, fimbriatae, aristatae, 1.3–2 mm longae. Chromosomatum numerus ignotus.

TYPE: **Bolivia:** Chuquisaca, Prov. Oropeza, Villa Maria, ca 10 km NE of Sucre, ca 2850 m, 12 Apr 1963, *D. Ugent & M. Cardenas 4944* (Holotype, WIS!).

DISTRIBUTION. Known only from the type locality where it was collected on the "margins of a weedy wheat field and surrounding thickets, with *Solanum boliviense, S. pachytrichum, Tagetes, Cerastium, Medicago, Rumex* and *Brassica,* 19° 1′S; 65° 10′ W". Figure 16.

The occurrence of *Galinsoga boliviensis* in a disturbed habitat and the weediness of the associated genera suggest that this species may also be weedy in the Bolivian Andes. Verification of this must await field studies, but the large number of heads per plant and the moderate number of achenes produced per head (ca 26)

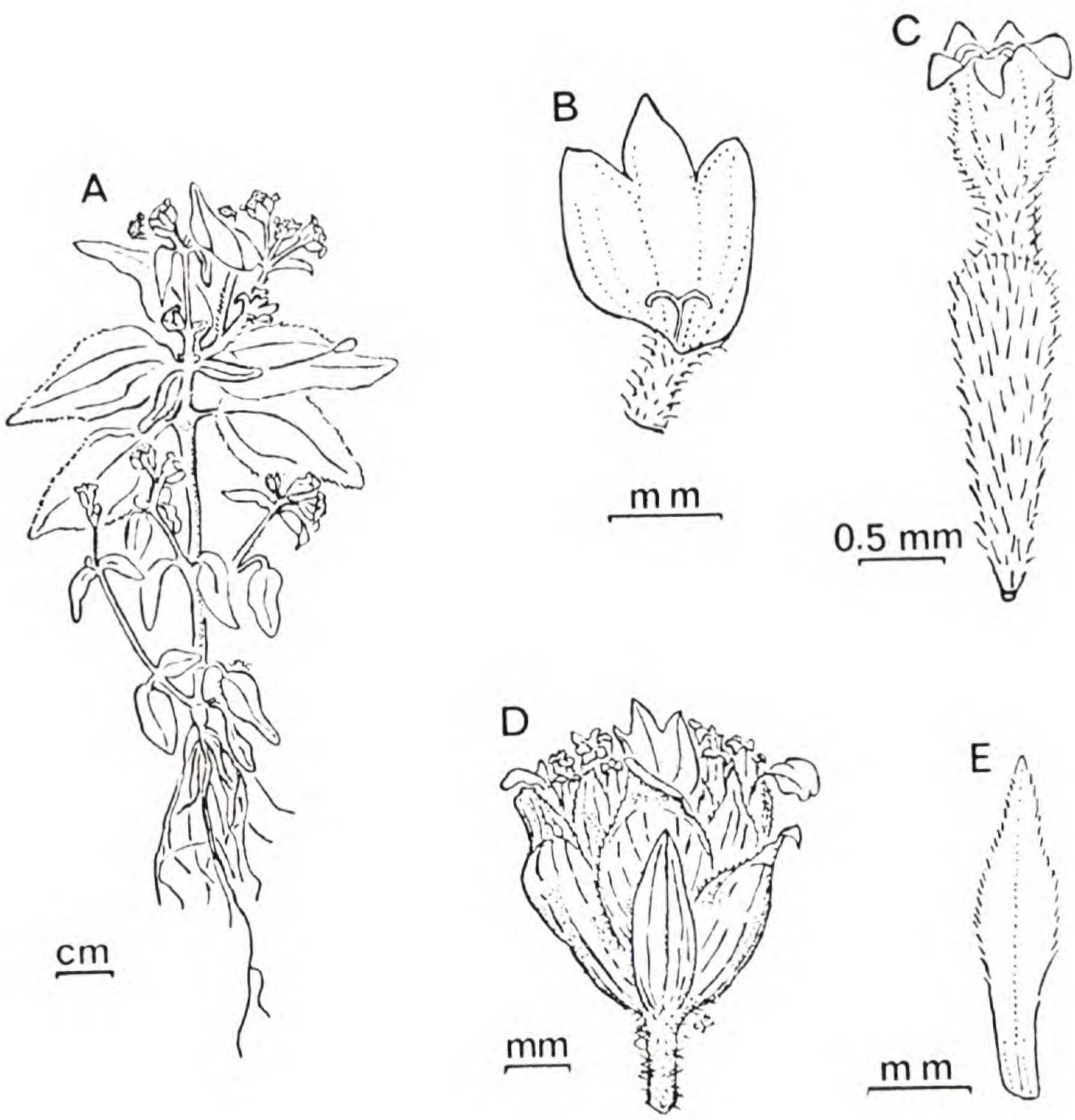

Figure 15. **Galinsoga boliviensis.** A, habit; B, ray corolla; C, disc floret; D, head; E, inner pale. All *Ugent & Cardenas 4944* (WIS).

represent a substantial reproductive potential. Judging from the presence of fully mature heads in addition to numerous buds in the capitulescence, it would appear that *G. boliviensis* flowers over an extended period of months as is true for other species in sect. *Galinsoga*. The specific epithet refers to this species' restricted distribution in Bolivia.

The short conical receptacle, nearly entire lanceolate pales, short disc corolla tube, aristate pappus scales, and the moderate to dense pubescence of the stem and peduncles are indicative of an alliance with *Galinsoga quadriradiata*.

Figure 16. **South American distributions of Galinsoga.** Map of northwestern South America indicating the distributions of *Galinsoga boliviensis* (star), *G. caligensis* (dots), and *G. mandonii* (diamonds).

11. **Galinsoga subdiscoidea** Cronquist, Mem. New York Bot. Gard. **12:** 288. *t. 2.* 1965. TYPE: **Mexico:** Durango, Sierra Madre Occidental, ca 10 mi W of El Salto, ca 8800 ft, 2 Oct 1962, *A. Cronquist 9583* (Holotype, NY!; isotypes, F, GH! MEXU, MICH! MO! MSC! TEX! US!).

Annual herbs, 2–12 cm tall. Stems nearly glabrous below to sparsely puberulent above. Leaves with blades tapering at the base and connate around the stem or with petioles to 1 mm long; blades elliptic, lanceolate, or oblanceolate, 4–22 mm long, 1–5 mm wide, with both surfaces puberulent, at the apex acute, at the base attenuate; margins entire to denticulate. Peduncles 0.5–8 mm long, puberulent. Heads 2–3.7 mm tall, 1.5–4.5 mm wide, often subtended by a bract, 3–6.5 mm long, 0.3–1.5 mm wide. Involucre subuniseriate, campanulate to hemispherical; phyllaries elliptic to ovate, 2–3.5 mm long, 0.8–1.7 mm wide, glabrous, greenish or deep purple, with the margins minutely laciniate and sometimes scarious. Receptacle ca 0.5 mm tall. Pales narrowly ovate, 2.2–3 mm long, 0.6–0.8 mm wide, entire or with 1–2 small, lateral lobes, at the apex acute to obtuse, outer pales weakly or not at all joined to adjacent phyllaries. Ray florets 0–5, corollas white or greenish; ligules lacking or 0.5–1 mm long, 0.2–0.5 mm wide, sometimes with small staminodes present, with the lobes 1–3, obtuse; tubes 0.8 mm long; achenes 1–1.2 mm long, 0.7–0.8 mm diam, strigose, at the apex truncate, pappus of 8–10 spathulate, fimbriate, yellowish scales to 1 mm long. Disc florets 11–20, corollas greenish-yellow; throats cupulate, 0.7–0.8 mm long, 0.8–1 mm diam, glabrous or sparsely minutely pilose near the tubes, with the lobes 5 or rarely 4, to 0.4 mm long, acute, recurved; tubes 0.5–0.8 mm long; anthers 0.5–0.6 mm long, with the appendage ovate; achenes and pappus like those of the ray. Chromosome number, $n = 8$.

DISTRIBUTION. Known from the Sierra Madre Occidental, state of Durango, Mexico near the towns of La Ciudad and El Salto (Figure 10), ca 2950 m. Flowering in September and October.

Galinsoga subdiscoidea, like most other Galinsogas, has a distribution in Mexico that falls within the range of *G. quadriradiata* and *G. parviflora. Galinsoga subdiscoidea* is particularly well distinguished from its Mexican neighbors by its diminutive habit and by the shapes of its leaves, disc corollas and pappus scales. The

disc corollas have a characteristic green color and the spathulate pappus scales are a distinctive pale yellow.

Two collections, *Cronquist 9586* (ENCB, GH, MICH, MO, TEX) and *Keil & Canne 8928* (OS), both collected just west of the town of El Salto, Durango, are especially interesting. The plants in these collections are 2.5–29 cm tall, have glandular capitate trichomes, achenes 1.3–2 mm long with oblanceolate disc pappus scales and a much reduced pappus on the ray achenes. Plants of the *Keil & Canne 8928* collection were counted as $n = 24$. Except for the deviation in chromosome number and the morphological features listed above, the plants from these two collections are clearly allied to *Galinsoga subdiscoidea,* specimens of which were collected at the same time in both instances. The broad, greenish disc corollas, oblanceolate, yellowish pappus scales, obpyramidal disc achenes, and narrow, subsessile leaves of these plants could be derived from only *G. subdiscoidea.* Both collections are interpreted to be of hybrid origin from a cross with *G. subdiscoidea* and another *Galinsoga.*

A likely possibility for the other parent is *Galinsoga quadriradiata,* which is common along roadsides near El Salto (*Keil & Canne 8889, 8890, 8943*). Features of the leaves, corollas and pappus which characterize the putative hybrid are intermediate between those of *G. subdiscoidea* and *G. quadriradiata.* The hexaploid condition in the hybrid may have been derived through allopolyploidy from the diploid *G. subdiscoidea* and the tetraploid *G. quadriradiata.* Verification of this presumed origin via greenhouse crosses and karyotype studies has been hindered because repeated atttempts to germinate achenes of *G. subdiscoidea* have failed.

The plants from the *Cronquist 9586* and the *Keil & Canne 8928* collections are interesting not only because of their apparent hybrid origin but also because they bear a striking resemblance to certain collections of *Galinsoga parviflora* from Arizona, New Mexico, and Chihuahua, Mexico (e.g., *Powell & Flyr 1499, Shinners 31049,* and *Pennell 19153*). These specimens of *G. parviflora* lack the characteristic glandular capitate trichomes, the cupulate and greenish disc corollas, and the yellow color of the disc pappus of the putative hybrid, but they approach the hybrid by having broader disc corollas than usual, broader pappus scales (but often acute and more numerous than those of the hybrid), and short stems with small, narrow leaves. The similarity between the hybrid and

the short-statured, small-leaved *G. parviflora* specimens raises the possibility that *G. parviflora* was involved in the cross with *G. subdiscoidea.* This origin would be unlikely, however, because both species are diploids. Further study is needed to determine the parentage and relationships of these hexaploid individuals.

SPECIMENS EXAMINED: **Mexico.** DURANGO: ca 37 km W of El Salto, *Cronquist & Fay 10784* (ENCB, MEXU, NY, US); 7.8 mi SW of La Ciudad, *Keil & Canne 8913** (OS); 4.8 mi SW of La Ciudad, *Keil & Canne 8917** (OS); 6.4 mi NE of La Ciudad, *Keil & Canne 8924** (OS); 15.6 mi NE of La Ciudad, *Keil & Canne 8928–1* (OS).

12. **Galinsoga mandonii** Sch.-Bip. Linnaea **34:** 529. 1866. TYPE: **Bolivia:** La Paz, Larecaja, vicinity of Sorata, 3200 m, Mar 1860, *G. Mandon 76* in part (non Feb 1859) (Holotype, P!, fragment of holotype, US!; isotypes, GH! NY!).

Galinsoga mandonii Sch.-Bip. Bull. Bot. Soc. France **12:** 80. 1865. *nom nud.*

Galinsoga unxioides Griseb. Symb. Fl. Argen. 198. 1879. TYPE: **Argentina:** Prov. Salta, "in radice montis Nevado del Castillo," 18 Mar. 1873, *E. G. Lorentz & G. Hieronymus 167* (Holotype, GOET?; isotypes, B, US!; photographs of B isotype, NY! US!).

Galinsoga calva Sch.-Bip. Bull. Bot. Soc. France **12:** 80. 1865. *nom. nud.* Based on *G. Mandon 80 & 81.* A fragment of *Mandon 80* at US is *G. mandonii.* The *Mandon 81* specimens at F, GH, MO, and P are all *G. quadriradiata,* but a specimen at NY is *G. mandonii.*

Galinsoga calva Rusby, Mem. Torrey Bot. Club **3:** 61. 1893. TYPE: **Bolivia:** Talca Chugiaguillo, Apr 1890, *M. Bang 809* (Holotype, NY!; isotypes, BM! GH! MICH! MO! US (2)!). The *Bang 809* specimens were distributed as *Galinsoga calva* Sch.-Bip., a *nomen nudum.* Rusby cited one additional collection, that of *Bang 1148* collected in the vicinity of Cochabamba in 1891. This collection was cited secondarily by Rusby and does not represent a syntype.

Stemmatella congesta Wedd. ex O. Hoffm. Natürl. Pflanzenfam. **4**(5): 231. 1890. TYPE: **Bolivia:** La Paz, Larecaga, vicinity of Sorata, *s.d., G. Mandon 293* (Holotype, P; isotypes, K, NY! US!; fragment of K isotype, GH!).

Galinsoga purpurea St. John & White, Rhodora **22:** 98. 1920. TYPE: **Bolivia:** Cochabamba, Bolivian Plateau in the vicinity of Cochabamba, 1891, *M. Bang 1148* (Holotype, GH!; isotypes, MO! US!).

Annual herbs, 1.5–66 cm tall. Stems simple or branched, internodes often elongate, pilose throughout with appressed to spreading aglandular and a few glandular capitate trichomes to 1 mm long, or rarely glabrous. Leaves sessile or with petioles to 1 cm long, green or deep purple, pilose; blades narrowly ovate to lanceolate, 0.5–5 cm long, 0.3–3.5 cm wide, with both surfaces pilose, at the apex acute, at the base rounded to attenuate; margins ciliate, remotely denticulate to coarsely serrate. Peduncles absent or rarely

to 1.8 cm long, pilose with appressed aglandular trichomes or with spreading glandular capitate trichomes intermixed. Heads 2.5–5 mm tall, 2–6.5 mm wide, in dense clusters subtended by narrowly ovate to lanceolate, attenuate, pilose bracts, 2–20 mm long, 0.6–6 mm wide. Involucre hemispherical to narrowly campanulate; outer phyllaries 2–3, 1.5–3 mm long, 0.8–2 mm wide, glabrous, with the margins entire or ciliate, narrowly scarious or herbaceous, green to deep purple; inner phyllaries ovate to ovate-deltoid, 2.6–3.6 mm long, 1.2–3.5 mm wide, glabrous or sparsely pilose, at the apex green to purple, with the margins minutely laciniate above the middle, entire and scarious below the middle. Receptacle 0.5–1.4(–1.7) mm tall, 0.6–1 mm diam. Outer pales lanceolate to narrowly ovate, 2–4.4 mm long, 0.8–1.7 mm wide, entire to trifid, at the apex often purple, strongly or weakly joined in pairs at the base to an adjacent phyllary; inner pales lanceolate to oblanceolate, 2–4.2 mm long, 0.5–1.5 mm wide, shallowly to deeply trifid, at the apex acute to attenuate; pales occasionally absent in very small heads. Ray florets 3–9, usually 5, corollas white to deep purple; ligules 0.6–1.7 mm long, 0.4–2 mm wide or absent, obovate, with the lobes 2–3 and obtuse, or reduced to a single oblong lobe; tubes 0.8–1.1 mm long; achenes 1.6–2 mm long, 0.5–0.7 mm diam, glabrous or sparsely strigose at the apex, epappose or with a pappus of 1–5 unequal, narrow, laciniate, acute to obtuse scales to 1 mm long. Disc florets ca 5–40, corollas yellow or purple; throats 0.8–1.2 mm long, 0.4–0.6 mm diam, glabrous or minutely pilose, with the lobes 0.2–0.5 mm long, tubes 0.5–0.6 mm long; anthers 0.5–0.6 mm long, with the appendage elliptic; achenes obconical to obpyramidal 1.3–1.5 mm long, 0.5 mm diam, subterete, glabrous or strigose; epappose or with a pappus of 10–20 unequal, lanceolate, fimbriate, obtuse to aristate scales, 1.5–2 mm long. Chromosome number unknown.

DISTRIBUTION. Restricted to the Andean regions of Peru, Bolivia and northernmost Argentina (Figure 16), 2000–4300 m. Flowering from December to September.

A list of plants collected by Mandon was first published by Schultz-Bipontinus (1865) and included the holotype collection of *Galinsoga mandonii* but without description. Schultz-Bipontinus (1866) later published the same list of plants, but this time the holotype collection was indicated as: "*Galinsoga Mandonii* SZ. Bip.,

n. sp. (ach. Calva)." The short reference to smooth achenes is regarded as a diagnosis and, therefore, the name is validly published on the later date.

Most plants collected at elevations of 3,700 m or higher are either procumbent or less than 13 cm tall (e.g., *Pennell 13365, 13479, 13480; Buchtien 105, 4313, 9288; Tovar 212*). The capitula of these depressed, high altitude plants are very small (ca 2 mm wide) and often contain as few as five florets each. The receptacle is usually reduced to a convex structure only 0.5 mm tall, and the inner pales are sometimes lacking. These plants occur only at very high altitudes and throughout the range of *Galinsoga mandonii* in the Peruvian and Bolivian Andes. The plants appear to represent an ecotypic, morphological race which lacks geographical and phyletic unity and, therefore, is not formally recognized here.

Galinsoga mandonii is readily distinguished from other Galinsogas by its sessile, or nearly sessile, clustered heads; stout, blunt or acute pappus scales; dark reddish-purple phyllaries; and rather small sessile leaves separated by long internodes. *Galinsoga mandonii* appears most closely related to *G. parviflora.* Both species usually possess small shallowly lobed ligules and trifid pales, and are similar in pubescence and features of the phyllaries.

Two specimens, *Macbride 3178* and *Mandon 78*, are like *Galinsoga parviflora* in most morphological features but have the pappus and long internodes of *G. mandonii.* Both specimens may be of hybrid origin. Also, the *Tovar 296* collection is like *G. parviflora* in vegetative features but has the firm, acute pappus of *G. mandonii* and perhaps is a hybrid or product of hybrid backcross to *G. parviflora.*

SPECIMENS EXAMINED: **Argentina.** JUJUY: hills of Guairahuasi, *Cabrera & Hernandez 14018* (GH); La Quiaca, 21 Feb 1940, *Meyer s.n.* (GH); La Quiaca from Villazon, *Schreiter 10898* (GH). **Bolivia.** LA PAZ: *Buchtien 105, 699* (US); *Buchtien 4313* (NY); below Obrajes, *Buchtien 4315* (LL, US); *Buchtien 8616, 8617, 8618, 8619* (LL); Miraflores, *Buchtien 9185* (LL); near Miraflores, *Buchtien 9186* (LL); near Obrajes, *Buchtien 9286, 9287* (LL, US); mt. slope, *Buchtien 9288* (LL), *Buchtien 9289* (US); Miraflores, *Buchtien 9434* (LL, US); slopes near Obrajes, *Buchtien 9435, 9436* (LL, US); near La Paz, *Julio 230* (GH, US); vicinity of Sorata, *Mandon 76*, in part (MICH, MO, NY); Sorata, *Mandon 81* (NY). CHUQUISACA: Sucre, *Cardenas 572* (NY); Punilla, ca 15 km NW of Sucre, *Ugent & Cardenas 4925* (WIS); Villa Maria, ca 10 km NE of Sucre, *Ugent & Cardenas 4946* (WIS). COCHABAMBA: Forancali, *Cardenas 2440* (US); Cochabamba, *Julio 1179* (US); Cochabamba, 26 Mar 1892, *Kuntze s.n.* (NY). ORURO: Pazña, *Buchtien 1586* (US); Cotaña, *Buchtien 4795* (US). POTOSÍ: Potosí,

Cardenas 247 (GH). **Peru.** ANCASH: Tallenga, *Ferreyra 7489* (US); Chacchash, near Chiquian, *Ferreyra 7577* (US). CUZCO: near Tinta, Temple of Viracocha, *Cook & Gilbert 210* (US); Ollantaytambo, *Cook & Gilbert 368, 483, 526, 640* (US); Cuzco, *Gunther 11671* (US); ruins of Sacsahuaman, near Cuzco, *Ugent & Ugent 3761* (WIS); Sacsahuaman, *Vargas 2602* (F); Hda. C'uyo, *Vargas 11199* (US). HUANUCO: 15 mi SE of Huanuco, *Macbride & Featherstone 2101* (US); Mito, *Macbride & Featherstone 1582* (F, US). HUANCAVELICA: Checcyana, 4 km E of Conaica, *Tovar 185* (US); Bunbunya, *Tovar 212* (US). JUNIN: Tarma, *Kunkel 323* (US); Tarma, *Killip & Smith 21805* (F, NY, US); La Oroya, *Macbride & Featherstone 946* (F). LA LIBERTAD: Agallpampa, *López 864* (US). LIMA: Rio Blanco, *Killip & Smith 21741* (F, GH, NY, US); Matucana, *Macbride & Featherstone 149, 150, 315* (F, US); Viso, *Macbride & Featherstone 573* (F, US); near Chosica, *Weberbauer 5359* (F, GH, US). PUNO: Chuquibambilla, *Pennell 13365* (F, GH, NY, US); Araranca, *Pennell 13479* (F, GH, NY, US); *Pennell 13480* (F, NY); Lampa, *Ranto-Hind P660* (NY); Sicuani, *Ranto-Hind P692* (NY); Salcedo, *Soukup 845* (F, GH, UC, US); Juliaca, *Stafford 467* (F).

13. **Galinsoga parviflora** Cav. Icon. Descr. Pl. **3:** 41. *t. 281.* 1795. TYPE: seen by Cavanilles at the Botanic Garden in Paris, later at the Botanic Garden in Madrid, grown from seed sent from Peru by D. Dombey (Holotype, MA: photograph of holotype, OS!).

Galinsoga quinqueradiata Ruiz & Pavon, Syst. Veg. **1:** 198. 1798. *nom. superfl.* Based on the type of *Galinsoga parviflora* Cav.

Galinsoga parviflora Cav. f. *quinqueradiata* (Ruiz & Pavon) Thell. Allg. Bot. Z. Syst. **21:** 6. 1916. *nom. illegit.*

Wiborgia acmella Roth, Catal. Bot. **2:** 112. 1800. TYPE: known to Roth as a garden plant introduced from Peru and later recognized by Roth as a synonym of *G. parviflora* Cav. in Catal. Bot. **3:** 78. 1806 (Holotype destroyed). According to Dr. Karl Otto Meyer (*in litt.*), Roth's herbarium was originally at Staatliches Museum für Naturkunde und Voreschichte, Oldenburg, Germany, but was later transferred to Berlin and destroyed there during war.

Vigolina acmella (Roth) Poiret in Lamarck, Encyc. Meth. **8:** 613. 1808.

Wiborgia parviflora (Cav.) HBK. Nov. Gen. Sp. **4:** 256. 1818.

Galinsoga laciniata Retz. in D. G. F. Hoffm. Phytogr. Blätt. **1:** 46. 1803. TYPE: no data available, but the notation "HL" in Retizus' handwriting on the back of the type specimen is considered by botanists at LD to indicate that the plant had been grown at the Botanic Garden, Lund (Holotype, LD!).

Sabazia microglossa DC. var. *microglossa,* Prodr. **5:** 497. 1836. TYPE: **Mexico:** "in montanis circa Mexico ad S. Augustinum," 26 Aug 1827, *J. L. Berlandier 733* (Holotype, G-DC; photograph of holotype, US!).

Sabazia microglossa DC. *β puberula* DC. Prodr. **5:** 497. 1836. TYPE: **Mexico:** "circa Mexico in montanis," Sep 1827, *J. L. Berlandier 910* (Holotype, G-DC; photograph of holotype, US!).

Adventina parviflora Raf. New Fl. N. Am. **1:** 67. 1836. TYPE: unknown, not at PH. Rafinesque's description of *Adventina* and the specific description of *A. parviflora* leave no doubt that he was describing *Galinsoga parviflora* Cav.

Galinsoga parviflora Cav. var. *semicalva* A. Gray, Smithsonian Contr. Knowl.

5: 98. 1853. TYPE: **New Mexico:** Coppermines, 6 Oct 1851, *C. Wright 1268* (Holotype, GH!; isotypes, GH! MO! NY!).

Galinsoga semicalva (A. Gray) St. John & White, Rhodora **22:** 100. 1920.

Galinsoga hirsuta Baker, Curator's Rep. Thirsk Nat. Hist. Soc. 1861. 13. 1862. TYPE: **England:** Surrey, Kew Bridge, 1861, *A. Irvine s.n.* (Holotype, K). Dr. J. E. Lousley has seen the Irvine specimen and verified its identity as *G. parviflora* (*in litt.*).

Stemmatella sodiroi Hieron. Bot. Jahrb. Syst. **28:** 601. 1901. TYPE: **Ecuador:** "crescit in region interandina," Sodiro 31/1 (Holotype, B; fragment of holotype, (?) US!; photographs of holotype, NY! US!).

Galinsoga parviflora Cav. var. *genuina* Thell. f. *subeglandulosa* Thell. Allg. Bot. Z. Syst. **21:** 8. 1916. TYPE: **Switzerland:** Zurich, 1 Aug 1917, *A. Thellung s.n.* (Lectotype chosen, Z!).

Galinsoga parviflora Cav. var. *genuina* Thell. f. *parceglandulosa* Thell. Allg. Bot. Z. Syst. **21:** 8. 1916. TYPE: **Australia:** New South Wales, Cumberland Co., Erworben, 1913, *T. V. Alkin s.n.* (Lectotype chosen, Z!).

Galinsoga semicalva A. Gray var. *percalva* S. F. Blake, Jour. Wash. Acad. Sci. **30:** 472. 1940. TYPE: **Arizona:** Pima Co., Santa Rita Mts., 20 Sep-4 Oct 1902, *D. Griffiths & J. J. Thornber 162* (Holotype, US!; isotype, NY!).

Galinsoga sphaerocephala Jones ex S. F. Blake, Contr. U. S. Natl. Herb. **29:** 130. 1945. *nom. illegit.*

Galinsoga parviflora Cav. var. *adenophora* Thell. Allg. Bot. Z. Syst. **21:** 9. 1916. TYPE: **Brazil:** São Paulo, 17 Oct 1905, *A. Usteri s.n.* (Lectotype chosen, ZT!; isolectotype, P!).

Annual herbs (2–)10–60 cm tall. Stems green to reddish purple, sparsely spreading pilose below to moderately pilose near the peduncles, sometimes with glandular capitate trichomes intermixed on the uppermost branches. Leaves with petioles to 2.5 cm long; blades broadly to narrowly ovate to lanceolate-ovate, 1–11 cm long, 0.5–7.2 cm wide, at the apex acute to acuminate, at the base cuneate to rounded, with both surfaces sparsely to moderately pilose; margins ciliate, denticulate to coarsely serrate. Peduncles 0.1–4 cm long, moderately to densely pilose with appressed to spreading aglandular trichomes, sometimes with glandular capitate trichomes intermixed. Heads 3.5–5 mm tall, 2–6 mm wide. Involucre glabrous; outer phyllaries persistent, 2–3, unequal, elliptic, oblong to ovate, 1.2–2.2 mm long, 0.6–1.5 mm wide, with margins scarious; inner phyllaries 2.5–3.5 mm long, 1.3–2.6 mm wide, with the margins scarious. Receptacle 0.6–1.7 mm tall, 0.6–1.5 mm diam. Outer pales broadly elliptic to obovate, often 2–3 fused at the base or nearly to the apex and appearing as one, 2.2–2.5 mm tall, 1–2.5 mm wide, 1–4 lobed at the apex, strongly joined in groups of 2–3 at the base to an adjacent phyllary and these persistent; inner pales

obovate or sometimes lanceolate, 2–3.2 mm long, 0.4–1 mm wide, shallowly to deeply trifid, rarely bifid or entire, the innermost pales persistent. Ray florets 3–8, usually 5, with the corollas dull white to pink-purple or white with pink veins; ligules absent or to 1.5 (–2) mm long, 1.5 mm wide, obovate with 2–3 acute lobes or oblong and entire; tubes 0.8–1.1 mm long, achenes 1.5–2.5 mm long, 0.5–0.9 mm diam, glabrous or strigose at the apex, epappose or with a pappus of 5–8 ventral, unequal, narrow, laciniate scales to 1 mm long. Disc florets 8–50, throats 0.8–1 mm long, 0.5–0.7 mm diam, with the lobes 0.2–0.3 mm long, tubes 0.3–0.5 mm long, anthers 0.4–0.6 mm long, with the appendage oblong; achenes somewhat angular, 1.2–2 mm long, 0.5–0.7 mm diam, glabrous and epappose, or strigose and with a pappus of 15–20 oblong, deeply fimbriate, white or gray scales, to 1.9 mm long, at the apex usually obtuse, sometimes acute or acuminate. Chromosome number, $n = 8$.

DISTRIBUTION: A nearly world-wide weed occurring in disturbed habitats and agricultural areas in most temperate and subtropical areas of the New World, Europe, Asia, Africa and Australia (Figure 17), 40–3600 m. Flowering the year round where climate permits or until the first frost.

In his discussion of Asteraceae described by M. E. Jones, S. F. Blake (1945) accepted the name *Galinsoga sphaerocephala* Jones. However, Jones (1933, p. 79) had used the epithet "sphaerocephala" in a confusing set of sentences repeated here: "the ray flowers are white and very short; the pappus is of several oblong scales variously lacerate and pointed. My species, sphaerocephala exaristate, is epappose, but otherwise as in *G. parviflora* and has linear or very narrow leaves." As it appeared in print, Jones' term "sphaerocephala exaristate" would seem to be a polynomial and as such is invalid. The name *Galinsoga sphaerocephala* Jones ex S. F. Blake is also unacceptable as no Latin diagnosis was provided when Blake published in 1945. There are also herbarium specimens, which according to Blake (1945), were labeled by P. A. Munz. These bear the name *Galinsoga* "exaristata," which is the epithet Jones evidently intended to publish. Surely, Jones had in mind two taxa when he published his confusing statements noted above, and as Blake indicated, lines must have been lost when the type was set for the paper.

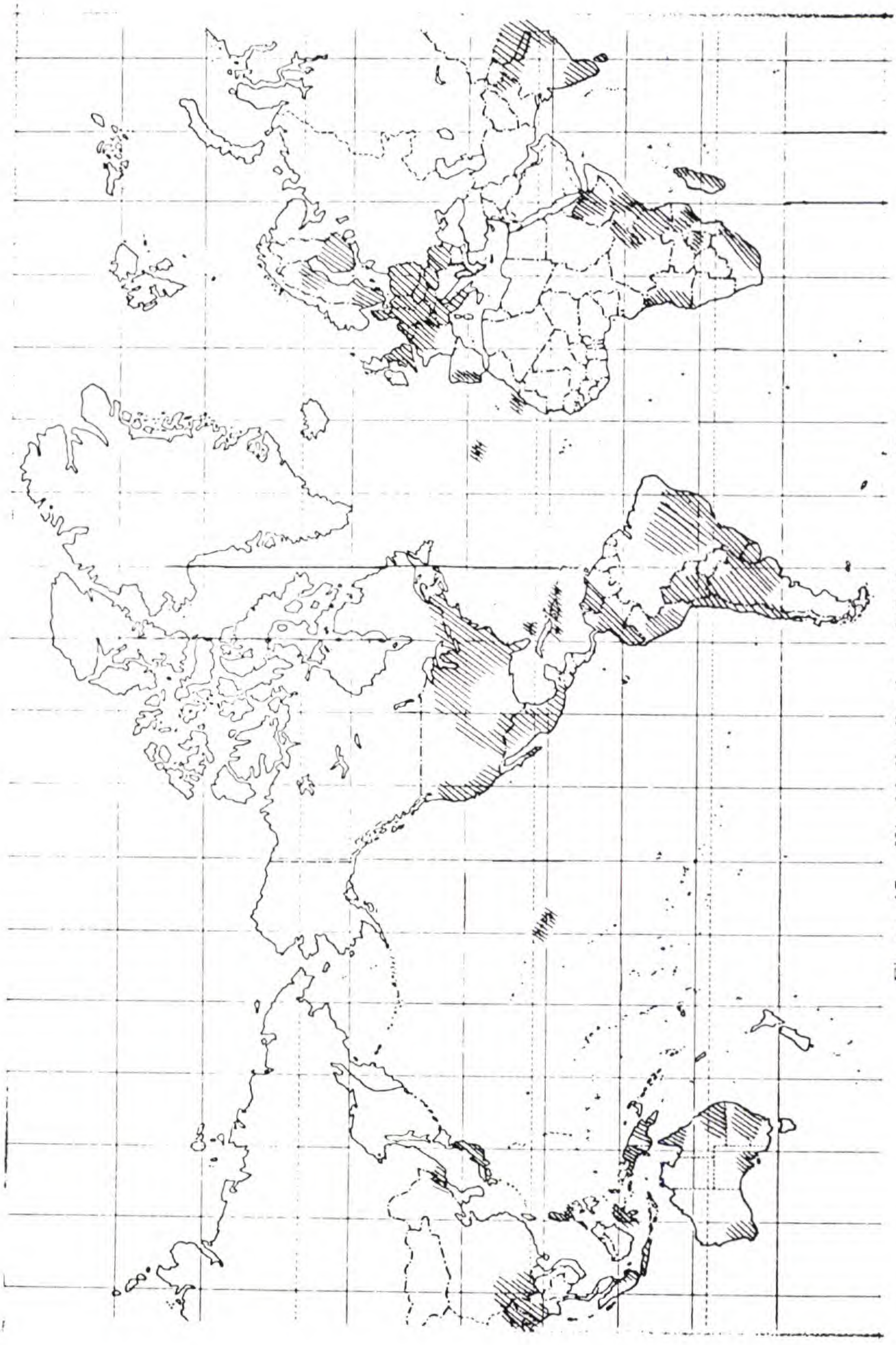

Figure 17. **World distribution of Galinsoga parviflora.**

Galinsoga parviflora is morphologically variable, as might be expected of a widespread weed. One of these variations was recognized by Gray (1853) as *G. parviflora* var. *semicalva* and is characterized by small leaves, usually 5 cm or less in length, somewhat campanulate-throated disc corollas, pappus scales shorter than the disc corolla, and pales more shallowly trifid than is typical. This form is concentrated in Arizona and New Mexico and the neighboring Mexican state of Chihuahua, areas where the more typical form of the species also occurs. Scattered collections are known from other Mexican states at elevations above 1500 m as far south as Distrito Federal. Plants with intermediate morphology are not uncommon.

Because this morphological form intergrades with the typical *Galinsoga parviflora* and its distribution is intermixed with that of the typical form, it is not distinguished as a well defined morpho-geographical unit. As a result, it is not worthy of formal varietal or specific status as has been held in the past (Gray, 1853; St. John & White, 1920). This variant seems best treated as a probable ecotype until field work and greenhouse studies can aid in the determination of morphological stability.

Galinsoga parviflora superficially resembles *G. quadriradiata* and the two have often been confused. They can be distinguished most readily by the characters outlined in Table 2.

Table 2.

Comparison of Galinsoga parviflora & Galinsoga quadriradiata.

G. parviflora	*G. quadriradiata*
1. Plants nearly glabrous to moderately pilose.	1. Plants moderately to densely pilose.
2. Outer phyllaries 2–4, scarious margined, persistent.	2. Outer phyllaries 1–2, margins herbaceous, deciduous.
3. Inner phyllaries and attached pales persistent.	3. Inner phyllaries and attached pales deciduous.
4. Inner pales deeply trifid, the middle lobe usually oblanceolate; late deciduous.	4. Inner pales usually entire, or weakly bifid or trifid; early deciduous.

5. Ray ligule absent to 1.5 (–2) mm long, dull white to pink.
6. Disc pappus of 15–20 blunt to acute, deeply fimbriate, white or gray scales, or absent.
7. Marginal cotyledonary hairs 40–80.
8. $n = 8$.

5. Ray ligule to 2.5 mm long, white to dark purplish-red.
6. Disc pappus of a few to 20 laciniate, acute to aristate, white scales or absent.
7. Marginal cotyledonary hairs 0–12.
8. $n = 16, 24, 32$.

When mixed populations of *Galinsoga parviflora* and *G. quadriradiata* were encountered in the field, neither morphological nor chromosomal indications of hybridization were observed. A widespread variant of *G. quadriradiata* (e.g., *Keil & Canne 9058, Orcutt 4349, Pringle 7345, Ton 1322*) does occur in central Mexico that has trifid pales rather like those in *G. parviflora* that might suggest hybridization, but in other respects this variant is good *G. quadriradiata* (see discussion under this latter species).

Although *Galinsoga parviflora* is known only as a diploid and *G. quadriradiata* only as a polyploid, there is no evidence to indicate that *G. parviflora* was involved directly in the origin of *G. quadriradiata*. A study by Haskell and Marks (1952) substantiates this theory. These authors observed mitotic metaphase figures of *G. parviflora* and *G. quadriradiata* (cited as *G. ciliata* (Raf.) S. F. Blake) and noted that the karyotype of *G. parviflora* contained a pair of metacentric chromosomes with satellites. These chromosomes were not present in the karyotype of *G. quadriradiata*. Conversely, the karyotype of *G. quadriradiata* contained a pair of chromosomes with elongate centric constrictions not present in *G. parviflora*.

REPRESENTATIVE SPECIMENS:[2] **Canada.** ONTARIO. Lanark Co.: Smiths Falls, *Shumovich & McCann 1462* (OAC). **Haiti.** ARTIBONITE: vicinity Ennery, *Leonard 9092* (GH, MO, US). **Mexico.** AGUASCALIENTES: 4 km W of Asientos, *Rzedowski 25066* (DS, MICH). BAJA CALIFORNIA: NE of La Carrerita, *Carter & Chisaki 3575* (DS, MEXU, MICH, UC). CHIHUAHUA: Memelichi, *Gentry 2742* (ARIZ, F, GH, MEXU, MO, UC, US). COAHUILA: Saltillo, *Palmer 790* in part (GH, MEXU, UC, US). COLIMA: without

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[2]*Canne* = *C*, *Canne & Hruschak* = *CH*, *Canne & Schunke* = *CS*, *Keil & Canne* = *KC*. Chromosome vouchers at OS are indicated by *($n = 8$).

locality, *Palmer 1244* (US). DISTRITO FEDERAL: 15 mi N of D.F.-Morelos boundary on Rte. 95d, *KC 9158*;* 28.3 mi N of Morelos-D. F. boundary, *KC 9161*;* 17.7 mi W of Mexico-D. F. boundary, *KC 9162**. DURANGO: 12 mi E of Durango, *Shreve 9163* (ARIZ, GH, MICH, UC). GUERRERO: Taxco, *Abbott 291* (ENCB). GUANAJUATO: 9 mi N of Querétaro state line, *Johnston 4031A* (MEXU, MICH, TEX). JALISCO: 25.8 mi SE of Magdalena Airport, *KC 9017–1* (OS); Atequiza, *KC 9028–1**. MEXICO: 33 mi E of Zitácuaro, *KC 9085–1*;* 3.7 mi W of El Yukon, *KC 9086*;* 6 mi W of Toluca, *KC 9087*;* 5 mi S of jct Rte. 15 & Rte. 55, *KC 9088*;* 0.8 mi S of Tenango, *KC 9090**. MICHOÁCAN: Vista Hermosa, *KC 9040*;* 0.8 mi SE of Ixtlán de los Boros, *KC 9042*;* 7.8 mi N of Zamora R.R. station, *KC 9045*;* 5.2 mi E of Morelia, *KC 9074**. MORELOS: N of Cuernavaca, *KC 9145–1*;* 5.5 mi N of Cuernavaca, *KC 9153**. NAYARIT: La Atarjea, *Mexia 882* (F). NUEVO LEON: Galeana, *Taylor 39* (ARIZ, DS, F, MO, NY, TEX, UC). OAXACA: San Andres Zautla, *Mendoza s.n.* (ENCB). PUEBLA: 2.5 mi E of Puebla-Mexico boundary on Rte. 190d, *KC 9166*;* 12.5 mi E of Puebla-Mexico boundary, Rte. 190d, *KC 9196*;* 33 mi E of Puebla-Mexico boundary, Rte. 190d, *KC 9171*;* jct Mex. Fed Rte. 190d and Rte. 140, *KC 9173*;* 1.3 mi E of jct Rte. 190d & Rte. 140, *KC 9174*;* SAN LUIS POTOSI: near San Luis Potosí, *Parry & Palmer 492* (F, GH, MO, NY, US). SONORA: El Bilito, NE of El Tigre, *White 4810* (MICH). VERACRUZ: 0.4 mi E of Puebla-Veracruz boundary on Rte. 150d, *KC 9175**. ZACATECAS: 6 mi S of Sierra Hermosa, *Shreve 8604* (ARIZ, US). **Puerto Rico.** Municipio Aduntas, Barrio de Guilarte, *Stimson & Montalvo 3928* (DUKE). **United States,** ARIZONA: Apache Co., near Greenlee Co. line on road to Blue, *Gould & Robinson 5129* (ARIZ, NY, UC). CALIFORNIA: Los Angeles Co., Vernon, *Braunton 716* (DS, GH, NY, UC, US). COLORADO: El Paso Co., 1 mi S of Pikeview, *Ewan 14590* (CAS). CONNECTICUT: Fairfield Co., Bridgeport, *Eames 1* (GH). HAWAII: Hawaii Co., Hawaii Volcanoes National Park, *Fosberg 53685* (NY, US). ILLINOIS: Cook Co., Chicago, *Chase 1179* (GH). INDIANA: Fayette Co., 2 mi E of Glenwood, *Friesner 18109* (GH, MICH, NY, TEX, US). KANSAS: Labette Co., bluffs 1 mi N of Oswego, *Rydberg & Imler 364* (NY). KENTUCKY: Jefferson Co., Bradstown, *CH 99–1**. MARYLAND: Frederick Co., Emmitsburg, *CH 141–1*. MASSACHUSETTS: Barnstable Co., Harwich, *Fernald & Long 17614* (GH). MICHIGAN: Branch Co., 1 mi E of Algansee, *Bennett 2646* (US, WIS). MINNESOTA: Hennepin Co., Minneapolis, *Moore 15647* (GH, MO, NY, UC, US). MISSOURI: Jackson Co., Independence, *Bush 406* (NY, US). NEBRASKA: Kearney Co., Minden, 10 Oct 1942, *Hapeman s.n.* (NY, UC). NEW JERSEY: Essex Co., East Orange, *Mackenzie 843* (ARIZ). NEW MEXICO: Lincoln Co., White Mts., *Wooton 501* (BM, NY, UC, US). NEW YORK: Albany Co., Albany, Sep 1867, *Clinton s.n.* (MSC, NY, US). NORTH DAKOTA: Cass Co., Fargo, *Stevens 2029* (NY, UC, US). OHIO: Fayette Co., Washington Court House, *CH 91–1**. OREGON: Multnomah Co.,Portland, *Brandegee s.n.* (GH). RHODE ISLAND: Providence Co., Providence, 18 Jun 1892, *Collins s.n.* (NY). TEXAS: Brewster Co., Chisos Mts., above Boot Springs, *Warnock 9740* (TEX). VERMONT: Chittenden Co., Burlington, Aug 1891, *Howe s.n.* (NY). VIRGINIA: Nelson Co., 5.9 mi N of jct VA 151 & VA 778, *CH 132*;* 7 mi S of jct VA 151 & VA 6, *CH 133–1**. WEST VIRGINIA: Pocahontas Co., 5 mi S of Frost, *CH 72**. **Argentina.** BUENOS AIRES: Villa Rosa, *Brizuela 1464* (TEX, US). **Bolivia.** COCHABAMBA: Cochabamba, *Shepard 266* (GH, US). **Brazil.** GOIAS: ca 5 km S of Corumba de Goias, *Irwin, Souza, & Reis dos Santos 10992* (GH, NY, TEX, US). **Chile.** VALDIVIA: Corral, *Gunckel 4829* (LL). **Colombia.** CAUCA: between Popayán and Cajeti, *Cuatrecasas 13827* (F, US).**Ecuador.** PICHINCHA: Quinto Airport, *C 282**. **Peru.**

CUZCO: Machu Picchu, *C 275**. HUANUCO: Concordia, *CS 196**; Chullqui, 116 km S of Tingo Maria, *CS 203b**; Cotosh, *CS 207**; La Esperanza, *CS 209b**, *CS 210**. JUNIN: Santa Rosa de Ocopa, ca 6 km N of Concepcion, *CS 239**; Concepcion, *CS 242**; ca 2 km N of Tarma, *CS 248**, *CS 250**, *CS 253**; Tarma, *C 258**; Acobamba, *CS 259**; Vilcabamba, *CS 260**; Cerro de Carpapata, *CS 262**. LIMA: Lima, *C 280**, *C 281**. **Uruguay.** CERRO LARGO: Palleros, *Gallinal, Aragone, Bergalli, Campal, & Rosengurtt PE-4558* (MO, NY). **Venezuela.** MERIDA: Mucuruba, *Gehriger 185* (F, NY, US).

Austria. LOWER AUSTRIA: Thernberg, *Dörfler & Dörfler* 3531 (DS). **Czechoslovakia.** CENTRAL BOHEMIA: Praha-Troja, Oct. 1937, *Deyl s.n.* (GH, UC, US). **Denmark.** JUTLAND: Vendsyssel, Skolehanen, 1 Aug 1930, *Kaad. s.n.* (DS). **East Germany.** BRANDENBURG: Brandenberg, 22 Jun 1900, *Gross s.n.* (NY). **Finland.** NYLANDI: without locality, 17 Aug 1953, *Fortelius s.n.* (FSU). **France.** BASSES-PYRENNEES: Bayonne, *Jallu 6918* (CAS). **Italy.** LOMBARDY: Lecco, 4 Sept 1888, *St. Lager s.n.* (NY). **Netherlands.** GELDERLAND: Wageninger, 8 Jun 1951, *De Vette s.n.* (UC). **Poland.** KRAKOW: Krakow, *Wroblowna 479* (DS, MO, UC, US). **Portugal.** BEIRA ALTA: without locality, *Rainha 5004* (US). **Romania.** OLTENIA: near Craiova, *Olaru & Paun 42* (NY). **Sweden.** STOCKHOLM: Stockholm, Aug 1888, *Thedenius s.n.* (NY). **Switzerland.** TICINO: Bellinzona, *Blake 9109* (LL). **England.** SURREY: Kew, *Nicholson 724* (GH). **Angola.** HUÍLA: **Humpata,** *Pritchard 309* (BM). **Ethiopia.** ERITREA: Asmara, *Pappi 2125* (A, F, MO, NY, US). **Kenya.** NAIROBI: Kismu, *Dummer 1963* (BM, MO). **Madagascar.** Without locality, *Decary 19582* (US). **Mozambique.** MOCAMBIQUE: Vila de Joao Belo, *Balsinhas 2* (BM). **Rhodesia.** MASHONALAND SOUTH: Salisbury, *Brain 4682* (MO). **South Africa.** GOOD HOPE: Grahamstown, *Schlechter 2638* (BM). **Zaire.** KIVU PARK: Rutshuru, *Ghesquiere 3567* (US). **Bhutan.** Tashi Gang Dzong, *Cooper 3121* (BM). **Burma.** ARAKAN: Mt. Victoria, *Cooper 6037* (UC). **Java.** PREANGER: Tjibodas, *Hallier 69* (NY). **India.** MADRAS: Attikan, *Barnes 526* (GH). **Japan.** TOKYO: Tokyo, 18 May 1912, *Fox s.n.* (BM). **Nepal.** DOLI DIST.: Masintola, *Ram 391* (NY). **Philippines.** LUZON: Baguio, *Clemens 18499* (BM, UC). **People's Republic of China.** SIKANG: K'angting, *Smith 10884* (A, BM, MO). **Tibet.** KONGBO: Tatakor, *Ludlow, Sherriff & Taylor 5450* (BM). **U.S.S.R.** PRIMORSK KRAG: Vladivostok and vicinity, *Topping 2473* (US). **Australia.** NEW SOUTH WALES: Kiama, Jan 1856, *Harvey s.n.* (GH). WESTERN AUSTRALIA: Perth, 24 Aug 1905, *Morrison s.n.* (A).

14. **Galinsoga glandulosa** Canne, sp. nov. Figure 18.

Herbae annuae, usque ad 30 cm altae. Caules erecti, ramosi, virides-rubri, pilosi trichomatibus effusis, glandulosis et eglandulosis. Folia petiolis 6–19 mm longis; laminae trullatae vel lanceolatae-ovatae, 1–3.5 cm longae, 0.5–2.5 cm latae, moderate pilosae utrinque; apice acuto, basi truncata; margines irregulariter dentati-serrati. Pedunculi 0.5–3 cm longi, effusi, glandulosi pilosi. Capitula 4–7 mm alta, 5–9 mm lata. Involucrum uniseriatum, campanulatum; phyllaria complanata vel convexa, elliptica-lanceolata 2.5–3.7 mm longa, 1–1.5 mm lata, pilosa, apice acuto et atroviridi, marginibus ciliatis. Receptaculum 1 mm altum, 1 mm diametro. Paleae ellipticae-rhombicae, 1.8–2 mm longae, 1.3 mm latae, ebur-

neae, complanatae vel convexae, marginibus ciliatis, apice abrupte acuminato vel infirme cuspidato. Flosculi radii 5, corollis albis; ligulae obovatae 2.5–3 mm longae et 1.5–2.5 mm latae, glabrae, lobis 0.3–0.6 mm longis, obtusis; tubi 1.3–1.8 mm longi, viriduli; achenia 1–1.2 mm longa, 0.5 mm diametro, strigosa, epapposa. Flosculi disci 15–20, corollis luteis; fauces 1.3–1.5 mm longae, 0.6–0.8 mm diametro, glabri, lobis 0.3–0.4 mm longis, acutis; tubi viriduli, 0.8 mm longi; antherae flavae, 1–1.2 mm longae, appendice ovata et 1–2 glandulis multicellulosis, clavatis; achenia acheniis radiorum similia. Chromosomatum numerus ignotus.

TYPE: **Mexico:** Querétaro, 23.5 mi SW of Xilitla on rd from Jalpan, ca 4500 ft, 9 Nov 1970, *G. L. Webster & G. J. Breckon 16367* (Holotype, DAV!; isotype, MICH!).

DISTRIBUTION. Known only from the type locality where it was collected on limestone in oak woods. Figure 10.

The presence of weakly cuspidate, whitish pales with ciliate margins and a pair of glands on the anther appendages (for which the species was named) mark *Galinsoga glandulosa* as a very distinct species. The relationship of *G. glandulosa* to other *Galinsoga* in sect. *Galinsoga* is obscure. The characters mentioned above plus the relatively long tube of the ray corollas are suggestive of *Tridax*. However, the disc and ray corolla shape, strigose achenes, short, yellow anthers, short, acute style branches, and leaf shape clearly exclude this species from *Tridax*.

EXCLUDED NAMES

Galinsogea alloeocarpa Spreng. Syst. Veg. **3:** 579. 1826. *nom. illegit.* Based on *Allocarpus caracasanus* HBK. Nov. Gen. Sp. Pl. **4:** 291. *t. 395.* 1818. TYPE: **Venezuela:** near Caracas, 450 hex., Nov 1799-Feb 1800, *F. H. A. von Humboldt & A. J. Bonpland s.n.* (Holotype, P). The description and illustration provided by HBK. exclude the taxon from *Galinsoga* because of its woody stem, corolla shape, and pappus type. The species is best placed in *Calea* as suggested by O. Kuntze, Rev. Gen. **1:** 324. 1891.

Galinsogea angustifolia Spreng. Neu. Entd. **2:** 138. 1820. TYPE: **Brazil:** *s.d., Otto s.n.* (Holotype, P!; probable isotype, P!). = **Calea angusta** S. F. Blake, Contr. U. S. Natl. Herb. **26:** 258. 1930.

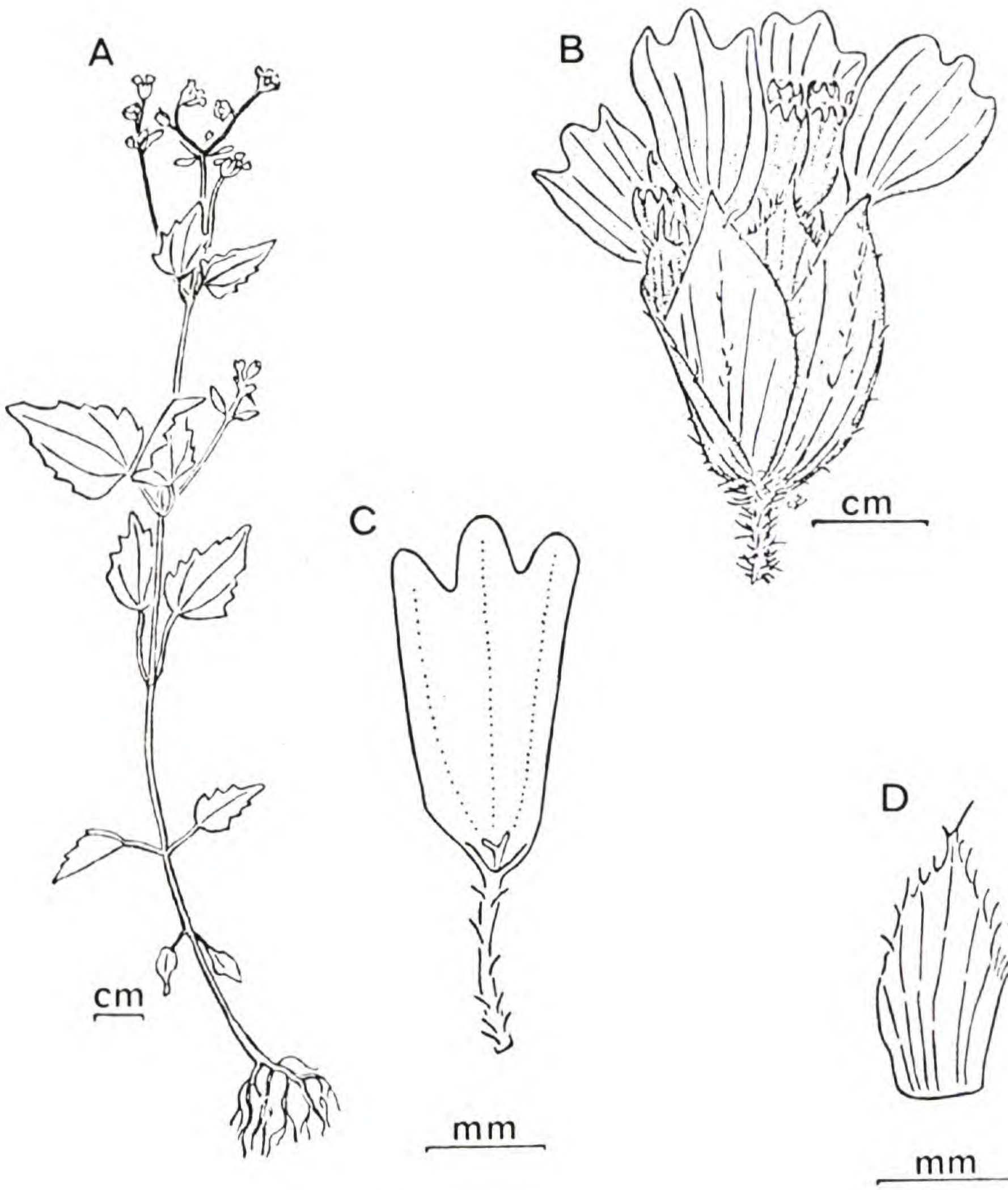

Figure 18. **Galinsoga glandulosa.** A, habit; B, head; C, ray corolla; D, pale. All *Webster & Breckon 16367* (MICH).

Galinsogea brachiata (Lag.) Spreng. Syst. Veg. **3:** 579. 1826. *Mocinna brachiata* Lag. Gen. et Sp. Pl. 31. 1816. TYPE: **Panama:** (Holotype, MA?). Sprengel's description of this shrub clearly excludes the taxon from *Galinsoga.* = **Calea brachiata** (Lag.) DC., *fide* DeCandolle (1836).

Galinsogea dentata Reichb. ex Steud. Nom. Bot. ed. 2. **1:** 656. 1840. *nom. nud.* = **Tridax trilobata** (Cav.) Hemsl. *fide* Powell (1965).

Galinsogea discolor Spreng. Syst. Veg. **3:** 577. 1826. *pro syn.* of *Verbesina atriplicifolia* Pers. TYPE: without data (Holotype, P!). = **Montanoa** sp.

Galinsogea linearifolia (Lag.) Spreng. Syst. Veg. **3:** 579. 1826. = **Gutierrezia linearifolia** Lag. Gen. et Sp. Pl. 30. 1816. *fide* Solbrig (1966). TYPE: "Hab. in N. H." (Holotype, MA?). Sprengel's description of this shrub eliminates it from *Galinsoga.*

Galinsogea megapotamica Spreng. Syst. Veg. **3:** 580. 1826. TYPE: **Brazil:** Rio Grande, *s.d., Sello s.n.* (Holotype, P). This taxon is removed from *Galinsoga* by virtue of its linear, 3 parted leaves as described by Sprengel.

Galinsoga ? oblongifolia (Hook.) DC. Prod. **5:** 677. 1836. *Wiborgia ? oblongifolia* Hook. Bot. Misc. **2:** 226. 1831. TYPE: **Peru:** Lima, Lurin, *s.d., A. Crickshanks s.n.* (Holotype, GL, photograph, US!). = **Eclipta alba** (L.) Hassk.

Galinsogea resinosa Hook. & Arn. Bot. Beechey's Voyage. 32. 1830. TYPE: **Chile:** Coquimbo, *s.d., T. Bridges s.n.* (Holotype, GL, photograph, K!). = **Gutierrezia resinosa** (Hook. & Arn.) S. F. Blake, Contr. U. S. Natl. Herb. **26:** 232. 1930. *fide* Solbrig (1966).

Galinsogea serrata (Lag.) Spreng. Syst. Veg. **3:** 579. 1826. *Mocinna serrata* Lag. Gen. et Sp. Pl. 31. 1816. TYPE: **Mexico:** near Salmanticam, *s.d., Nee s.n.* (Holotype, MA?). Sprengel's description of the species as shrubby with scabrous leaves excludes the taxon from *Galinsoga.*

Galinsoga trifida Pers. Synopsis Plantarum **2:** 472. 1807. TYPE: unknown, not at L. In the original description, the epithet "trifida" is preceded by an asterisk, and as Boivin (1962) and Chater and Brummitt (1966) have pointed out, it is not clear in the majority of cases whether Persoon was indicating subspecies or doubtful species by the use of the asterisk. Persoon described *G. trifida* as having narrow, trifid, lanceolate, dentate leaves. No Galinsogas have divided leaves. The description of *G. trifida* is preceded by one of *G. trilobata* Cav. and Persoon says of *G. trifida,* "Facie antecedentis," (1807, p. 472). Thus Persoon may have suggested that *G. trifida* has affinities with the genus *Tridax* to which *G. trilobata* was transferred by Hemsley (1881). As no

type was indicated and no probable type material has been located, it is not possible to determine the precise affiliation of *G. trifida.* The situation seems best handled by excluding the name from *Galinsoga* on the basis of Persoon's description.

Galinsoga trilobata Cav. Icon. Descr. Pl. **3:** 42. *t. 282.* 1795. TYPE: **Mexico.** (Lectotype, MA). = **Tridax trilobata** (Cav.) Hemsl. Biol. Centr. Amer. Bot.**2:** 208. 1881. *fide* Powell (1965).

Galinsogea uniflora Spreng. Syst. Veg. **3:** 580. 1826. TYPE: **Uruguay:** Montevideo, *s.d., Sello s.n.* (Holotype, P). Sprengel's description of this taxon with linear, scabrous leaves excludes this species from *Galinsoga.*

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DEPARTMENT OF BOTANY AND GENETICS
UNIVERSITY OF GUELPH
GUELPH, ONTARIO, CANADA N1G 2W1

WILLOWS OF THE ROCKY MOUNTAIN STATES

ROBERT D. DORN

About two-thirds of all willow (*Salix*) species occurring in the United States outside Alaska are found in the Rocky Mountain states. Treatments of the genus in state floras of this region are out-of-date and most contain significant errors. I recently completed a detailed study of one section of the genus (Dorn, 1975a), and during that study much data were obtained on other sections. Since it may be a considerable period before all the sections can be studied in detail, it is desirable to bring the taxonomy of Rocky Mountain willows up to date at this time and to point out the more important problems still remaining.

I have spent the last nine summers observing willows in the field from Alaska to Newfoundland south to California, Colorado, and Massachusetts. I have not had the opportunity for field study in much of California and the Southwest. Southwestern willows are included here because these species have diverged from each other more than those in most other areas and, thus, are easier to treat taxonomically.

This study is based on specimens in A, ARIZ, CAN, CS, DAO, F, GH, JEPS, K, MONT, MONTU, NA, NY, PH, RM, SASK, UC, and US (abbreviations follow Holmgren & Keuken, 1974). I have seen all the original descriptions, but I have not seen all the type specimens. The location of some types is still uncertain. Some early workers studied specimens in private and public herbaria all over Europe and based their descriptions of new species on some of these. Thus, locating a type specimen and designating lectotypes often require detailed study. Herbaria listed here are only for those types actually seen or for those with a reliable reference in the literature. Most species synonyms with type localities in the Rocky Mountain states are listed. Only a few of the many proposed infraspecific names are included. An evaluation of most of these must await further study. A number of chromosome counts were obtained, and these were reported elsewhere (Dorn, 1975a, 1975b, 1976). Moreover, the flavonoid chemistry of the leaves of many species was surveyed. Flavonoid profiles alone are of limited taxonomic value, as there may be more than one profile within a single apparent species, or different species may have the same profile and

the compounds may or may not be the same. Compounds were identified for eleven of the species (Dorn, 1975a; Argus, unpublished data). These data are most useful when used in conjunction with other data.

TERMINOLOGY

The terminology for *Salix* used here generally follows Argus (1973). Some of the terms, however, need elaboration. *Pruinose* refers to a bluish-white bloom on the branches which is rubbed off easily. *Glaucous* refers to a whitish wax on the underside of leaves which also can be rubbed off. This characteristic often appears granular under high magnification. Leaves of some species are merely pale beneath but lack the whitish wax. A *floriferous* branchlet is a branchlet which bears flowers. Its length is measured from its growing point of the season to the lowermost flower bract (which may actually lack a flower). This is equivalent to the term peduncle of many authors. *Bract* refers to the foliar structure (seldom green) subtending each flower. Some authors use the term scale for this structure. The *stipe* is the stalk of the pistil. Pedicel is the older, equivalent term.

MORPHOLOGY

There appear to be exceptions to the usual situation in all morphological characteristics, at least when considering the genus as a whole. Some characteristics are much more constant than others, and some that are constant in one section may be variable in another. This has been a source of much confusion in the past.

In the Rocky Mountain states, the distinction of the two subgenera, *Salix* and *Vetrix,* is very sharp if persistence of the fruiting bracts is employed. In the primitive subg. *Salix,* the species have deciduous fruiting bracts while in subg. *Vetrix* the fruiting bracts are persistent. The native sections of subg. *Salix* are also easily separated. The species of sect. *Humboldtianae* have the unique feature of bud scales with free overlapping margins. In other sections the margins are fused to form a cap-like bud scale. Species of sect. *Salicaster* have mostly lanceolate to ovate leaves and three or more stamens, while those of sect. *Longifoliae* have two stamens and predominantly linear leaves. Species of sect. *Salix* are introduced trees with mostly lanceolate or lance-linear leaves and mostly two stamens.

The sections of the more advanced subg. *Vetrix* are not so easily separable. The most constant characteristics are leaf glaucescence and capsule pubescence, but these cut across sectional lines. Number and position of nectaries and presence or absence of stomata on the upper leaf surface, characteristics that were frequently used by Schneider (1921), have a relatively poor constancy. Leaf shape and size, often used by Ball (1952), are also not very constant. Some characteristics are often quite constant but are difficult to describe. These include the degree and pattern of cracking or furrowing of the bark of older branches (often lacking on herbarium specimens), leaf color and texture, and venation pattern in leaves.

TAXONOMY

Keys to staminate and vegetative material are extremely difficult to construct for more than about 20 species, or fewer when they are closely related. The best way to identify staminate material is to compare it (flower bracts, leaves, branchlets, buds) with pistillate material collected from the same area. Ideally, both staminate and pistillate plants should be tagged and mature leaves collected later, particularly for species with precocious aments. Sequential collections from the same plant are always easier to identify. When collecting specimens, it is desirable to obtain growth three or four years old. Important data to record are height, habitat, elevation, and presence or absence of glaucescence on the underside of the leaves at time of collection. It is desirable to note associated *Salix* species in case a question of hybridization arises. However, hybridization is extremely difficult to prove in wild individuals, and it is certainly uncommon in the Rocky Mountain states. Flavonoid chemistry studies have shown that suspected hybrids based on morphological characteristics were simply morphological variants of a single species (Dorn, 1975a).

Due to the great morphological variability of willows, it is not practical to take into account all of the exceptions when constructing a key for identification. If they were taken into account, we would have a series of contrasting descriptions. A compromise attempts to maximize correct determinations while avoiding undue length and complexity. A correct determination can be expected over 95 percent of the time with the pistillate key if good, mature specimens are available. The percentage will be lower with the staminate key.

The sectional classification follows my synopsis of American willows (Dorn, 1976). Additional discussion and references appear in that paper. The area included in this treatment covers the states of Idaho, Montana, Wyoming, Colorado, Utah, Nevada, Arizona, and New Mexico and the Black Hills area of South Dakota. In most cases, descriptions apply only to plants of this area. Distribution is first given for this area only, followed by distribution outside this area, if known from elsewhere.

KEY TO PISTILLATE WILLOWS OF THE ROCKY MOUNTAIN STATES

1. Bracts subtending flowers usually yellowish, green, or white (tan), deciduous by the time capsules are mature; styles 1 mm or less long; plants often trees, native or introduced (Subg. *Salix*). ..... 2.
   2. Leaf blades mostly linear or nearly so, rarely narrowly elliptic; styles 0.2 mm or less long; bud scales without free overlapping margins. ..... 3.
      3. Leaf blades 0.5–3.5 cm long; pistillate aments 0.7–2 cm long; capsules pubescent; S Arizona & New Mexico. ..... 11. *S. taxifolia.*
      3. Leaf blades 2–13 cm long; pistillate aments 1.5–6 cm long; capsules glabrous or pubescent. ..... 4.
         4. Leaves green on both sides, often pubescent; flower bracts lanceolate or lance-linear, pubescent or sometimes glabrate. ..... 12. *S. exigua.*
         4. Leaves usually glaucous or glaucescent beneath, glabrous when expanded; flower bracts usually broader, glabrous or sometimes pubescent at base. ..... 13. *S. melanopsis.*
   2. Leaf blades lance-linear or broader; styles 0–1 mm long; bud scales with or without free overlapping margins. ..... 5.
      5. Bud scales with free overlapping margins, usually pointed at tip. .. 6.
         6. Leaf blades green above and beneath or slightly more pale beneath but not glaucescent. ..... 2. *S. gooddingii.*
         6. Leaf blades glaucous or glaucescent beneath. ..... 7.
            7. Latest developing leaves narrowly lanceolate, the margins gradually tapering to tip (straight sides), somewhat coriaceous; capsules usually ovate in outline. ..... 1. *S. bonplandiana.*
            7. Latest developing leaves lanceolate to ovate, the margins somewhat abruptly tapering to tip (sides incurved just before tip), not coriaceous; capsules lanceolate in outline. ..... 3. *S. amygdaloides.*
      5. Bud scales without free overlapping margins, usually rounded at tip... 8.
         8. Leaf blades glaucous or glaucescent beneath. ..... 9.
            9. Branchlets very long and hanging straight downward (weeping willow). ..... 10. *S. babylonica.*
            9. Branchlets short or long, erect to ascending. ..... 10.
               10. Margins of leaves of floriferous branchlets weakly or not at all glandular; introduced trees. ..... 11.
                  11. Twigs brittle at base, easily broken off; leaves glabrous when expanded (crack willow). ..... 9. *S. fragilis.*

11. Twigs not brittle at base; leaves often pubescent (white willow). ..... 8. *S. alba.*
10. Margins of leaves of floriferous branchlets usually strongly glandular; native trees or shrubs. ..... 12.
12. Capsules mostly 7 mm or less long, usually dull, maturing in spring (March-June); pistillate aments 2–8 cm long. ..... 7. *S. lasiandra.*
12. Capsules mostly 7–11 mm long when mature, somewhat shiny, maturing in summer (July-September); pistillate aments 2–4 cm long. ..... 5. *S. serissima.*

8. Leaf blades green on both sides or slightly more pale beneath but not glaucescent. ..... 13.
13. Plants introduced trees, not known to escape cultivation. ..... 4. *S. pentandra.*
13. Plants native shrubs or trees. ..... 14.
14. Capsules mostly 7–11 mm long when mature, somewhat shiny, maturing in summer (July-September); pistillate aments 2–4 cm long. ..... 5. *S. serissima.*
14. Capsules mostly 7 mm or less long, usually dull, maturing in spring (March-June); pistillate aments 2–8 cm long. . 15.
15. Leaf blades mostly about 3 times as long as wide; South Dakota & E Colorado. ..... 6. *S. lucida.*
15. Leaf blades mostly 4 or more times as long as wide. ..... 7a. *S. lasiandra* var. *caudata.*

1. Bracts subtending flowers usually brown, black, or reddish, rarely yellowish or greenish, persistent; styles 0–3 mm long; native shrubs, rarely tree-like (Subg. *Vetrix*). ..... 16.
16. Capsules glabrous. ..... 17.
17. Plants creeping, 1–3 cm high, the leaves 7(–9) mm or less long, near or above timberline. ..... 16. *S. rotundifolia.*
17. Plants usually upright, mostly over 20 cm high, the larger leaves usually well over 10 mm long; most species below timberline. ..... 18.
18. Leaves glaucous or glaucescent beneath (rarely not expanded in fruit). ..... 19.
19. Styles averaging 0.7 mm or less long. ..... 20.
20. Stipes 2–4 mm long; leaf blades oblong, oblanceolate, or narrowly obovate, somewhat leathery, entire; N Idaho. ..... 17. *S. pedicellaris.*
20. Stipes sometimes as much as 2 mm long but then the leaf blades not as above. ..... 21.
21. Plants of the mountains of Idaho, Montana, & NW Wyoming; leaf blades glabrous and entire (or a few serrulate), elliptic to elliptic-obovate; floriferous branchlets (3)5–15 mm long; stipes 0.3–1.5(2) mm long. ..... 34. *S. farriae.*
21. Plants without characters combined as above. ... 22.
22. Twigs usually pruinose, especially at nodes; stipes 0.3–1 mm long. ..... 31. *S. irrorata.*

22. Twigs not pruinose; stipes 0.5–4.5 mm long.. 23.
    23. Stipes of normally developed capsules 2–4.5 mm long; leaves usually toothed; plains or mountains. . . . . 43. *S. lutea.*
    23. Stipes 0.5–2 mm long; leaves often entire; along streams in deserts, plains, and foothills. . . . . 24.
        24. Leaf blades oblanceolate or oblong to obovate, dark green above, white-glaucous beneath; SW Idaho, Nevada, Arizona, S Utah, & W New Mexico. . . . . 32. *S. lasiolepis.*
        24. Leaf blades narrowly elliptic or lanceolate, dull green above, light bluish-green beneath; Nevada, Arizona, Utah, New Mexico, Colorado, & SE Wyoming. . . . . 44. *S. ligulifolia.*
19. Styles averaging over 0.7 mm long. . . . . 25.
    25. Plants of S Wyoming, Colorado, Utah, Arizona, & New Mexico. . . . . 42. *S. monticola.*
    25. Plants of N Wyoming, South Dakota, Montana, & Idaho. . . . . 26.
        26. Leaf blades glabrous, entire (rarely a few serrulate), elliptic to elliptic-obovate; floriferous branchlets (3)5–15 mm long. . . . . 34. *S. farriae.*
        26. Leaf blades pubescent at least when young, toothed, the shape various; floriferous branchlets 0–30 mm long. . . . . 27.
            27. Floriferous branchlets (5)10–30 mm long. . . . . 35. *S. barclayi.*
            27. Floriferous branchlets 0–8(12) mm long. . . . . 28.
                28. Aments, or some of them, at tips of twigs of previous year; styles 1–3 mm long; leaves very finely glandular-toothed. . . . . 48. *S. tweedyi.*
                28. Aments not at tips of twigs; styles 0.5–1.8 mm long; leaves crenate-serrate. . . . . 33. *S. pseudomonticola.*
18. Leaves not glaucous or glaucescent beneath. . . . . 29.
    29. Plants of east-central Arizona. . . . . 41. *S. arizonica.*
    29. Plants of Colorado, Utah, Nevada & northward. . . . . 30.
        30. Styles 1–3 mm long; some aments at tips of twigs of previous year; leaves very finely glandular-toothed. 48. *S. tweedyi.*
        30. Styles 0.2–1.5 mm long; aments not at tips of twigs; leaves various. . . . . 31.
            31. Aments mostly 0.8–2 cm long; stipes 0–0.8 mm long; plants mostly less than 2 m high; Colorado, Utah, Nevada, Wyoming, Idaho, & SW & C Montana. . . . . 37. *S. wolfii.*

31. Aments mostly (1)2–9 cm long; stipes (0.3)0.5–4 mm long; plants 0.2–6 m high. . . . . 32.
    32. Leaves of floriferous branchlets little if at all reduced, the branchlets 8–30 mm long; leaf blades mostly ovate, broadly elliptic, or obovate, often densely pubescent with long, loose hairs; Idaho & W Montana. . . . . 36. *S. commutata*.
    32. Leaves of floriferous branchlets usually much reduced, the branchlets (1)2–10(15) mm long; leaf blades mostly lanceolate, narrowly elliptic, or oblanceolate, rarely ovate or obovate, variously pubescent or glabrous. . . . . 33.
        33. Leaves thin and somewhat translucent; stipes (1.5)2–4 mm long; styles 0.2–0.7(1) mm long; NW Wyoming, Montana & Idaho. . . . . 45. *S. monochroma*.
        33. Leaves thickish; stipes 0.5–2(2.5) mm long; styles 0.3–1.2(1.5) mm long. . . . . 40. *S. boothii*.
16. Capsules pubescent. . . . . 34.
    34. Plants creeping shrubs 1–8 cm high, near or above timberline. . . . 35.
        35. Leaf tip usually rounded or obtuse; leaves glaucous and prominently reticulate-veined beneath; styles less than 0.5 mm long; nectaries 2. . . . . 15. *S. reticulata*.
        35. Leaf tip usually pointed; leaves glaucous or not beneath, usually not reticulate-veined; styles 0.3–2 mm long; nectary 1. . . . . 36.
            36. Leaf blades mostly elliptic to oval, glaucous beneath, those of previous year usually not persisting; pistillate aments 1–5 cm long. . . . . 20. *S. arctica*.
            36. Leaf blades narrowly elliptic to elliptic, usually green beneath, those of previous year often persisting; pistillate aments mostly 0.6–2 cm long. . . . . 21. *S. cascadensis*.
    34. Plants erect shrubs or trees mostly over 20 cm high (*S. glauca* & *S. vestita* rarely creeping), only rarely above timberline. . . . . 37.
        37. Twigs of previous year (and sometimes those of season) pruinose, sometimes only apparent at nodes especially behind buds. . . . 38.
            38. Aments 8–20(25) mm long (if to 40 mm, the leaves glabrous or puberulent), loosely flowered, usually with leafy floriferous branchlets 2–18 mm long; stipes 1–3 mm long (as little as 0.5 mm in specimens with glabrous or puberulent leaves). . . . 39.
                39. Leaves sericeous on both sides, obscurely if at all glaucous; bracts usually brown or tan, mostly twice or more as long as wide. . . . . 24. *S. geyeriana*.
                39. Leaves with few hairs beneath and glaucous; bracts usually blackish, mostly less than twice as long as wide. . . . . 25. *S. lemmonii*.
            38. Aments 15–60 mm long, densely flowered, sessile or nearly so; stipes 0.1–0.8 mm long; leaves usually silvery-pubescent be-

neath. . . . . 29. *S. drummondiana.*
37. Twigs not pruinose (rarely so in *S. planifolia*). . . . . 40.
40. Leaf blades elliptic-obovate to oval, dark green above, silvery-hairy beneath (becoming glabrate); some aments at tips of shoots of season; Montana. . . . . 14. *S. vestita.*
40. Leaf blades not as above; aments usually not at tips of shoots of season (on branchlets with no or reduced leaves). . . . . 41.
41. Leaf blades narrowly elliptic, oblong, or oblanceolate (sometimes obovate in NW Montana, N Idaho, & W Nevada), usually densely white- or silvery-hairy beneath, glabrous or glabrate and green above; stipes 1 mm or less long. . . . . 42.
42. Leaves white-hairy beneath; twigs pubescent. . . . . 30. *S. candida.*
42. Leaves silvery-hairy beneath; twigs glabrous or pubescent. . . . . 43.
43. Pistillate aments sessile or nearly so; widespread. . . . . 29. *S. drummondiana.*
43. Pistillate aments with leafy floriferous branchlets 5–20 mm long; NW Montana, N Idaho, & W Nevada. . . . . 46. *S. sitchensis.*
41. Leaf blades often broader, not densely white- or silvery-hairy beneath, or if so, then similar above (rarely not expanded in fruit); stipes various. . . . . 44.
44. Leaves equally green on both sides, pubescent. . . 45.
45. Styles 1–2.5 mm long; twigs glutinous; aments sessile or nearly so, some at tips of twigs of previous year. . . . . 47. *S. barrattiana.*
45. Styles 0.2–1.5 mm long; twigs not glutinous; aments not at tips of twigs, subsessile or with floriferous branchlets to 25 mm long. . . . . 46.
46. Aments 1–5 cm long; either the young leaves with prominently glandular margins or the capsules mostly 7 mm or more long. . . . . 47.
47. Mature capsules 3–4(7) mm long; some smallest leaves, especially those on floriferous branchlets, with conspicuous glands which extend out beyond margin at a right angle. . . . . 39. *S. eastwoodiae.*
47. Mature capsules mostly over 7 mm long; leaves rarely glandular as above. . . . . 38. *S. orestera.*
46. Aments 0.8–2 cm long; young leaves usually lacking glands on margins; capsules usually less than 6 mm long. . . . . 37. *S. wolfii.*
44. Leaves white-glaucous or otherwise lighter beneath, glabrous or pubescent (rarely not expanded in fruit). . . . . 48.

48. Styles 1–2.5 mm long; twigs glutinous; aments sessile or nearly so, some at tips of twigs of previous year; Montana & Wyoming. 47. *S. barrattiana.*
48. Styles 0.1–1.5 mm long; twigs not glutinous; aments sessile or on floriferous branchlets to 25 mm long, not at tips of twigs of previous year. 49.
49. Leaf blades mostly 5 or more times as long as wide, usually sharply serrate; styles 0.1–0.3 mm long; South Dakota, Montana, & Colorado. ..... 23. *S. petiolaris.*
49. Leaf blades rarely as much as 5 times as long as wide, entire or bluntly toothed; styles 0.1–1.5 mm long. ..... 50.
50. Stipes mostly 2–5 mm long; styles 0.4 mm or less long; flower bracts light brown or yellowish. ..... 22. *S. bebbiana.*
50. Stipes 3 mm or less long; styles 0.1–1.5 mm long; flower bracts yellowish or light brown to black. .....
51. (Couplet moved to left margin of key.)

51. Aments mostly appearing with the leaves, on leafy floriferous branchlets 2–25 mm long. ..... 52.
52. Leaf blades glabrous or puberulent; plants to 5 m high. ..... 25. *S. lemmonii.*
52. Leaf blades obviously pubescent (rarely glabrous in plants to 1.5 m high). 53.
53. Leaf blades oblanceolate to elliptic; stipes 0.5–2 mm long; W Nevada. ..... 38. *S. orestera.*
53. Leaf blades elliptic to elliptic-obovate or oblong; stipes 0–1.5 mm long; not known from Nevada. ..... 54.
54. Aments 0.5–2 cm long; floriferous branchlets 2–10 mm long; stipes less than 0.5 mm long; petioles mostly 1–3 mm long. ..... 18. *S. brachycarpa.*
54. Aments (1.5)2–5 cm long; floriferous branchlets 5–25 mm long; stipes 0–1.5 mm long; petioles often over 3 mm long. ..... 19. *S. glauca.*

51. Aments mostly appearing before the leaves, sessile or subsessile (rarely on mostly naked branchlets to 13 mm long). ..... 55.
55. Stipes 0–1 mm long; stigmas usually less than 0.5 mm long; twigs of previous year often reddish and shiny. ..... 28. *S. planifolia.*
55. Stipes (0.8)1–3 mm long; stigmas usually over 0.5 mm long; twigs of previous year yellowish to reddish-brown, dull. ..... 56.
56. Twigs of previous year glabrous; leaves, if present, elliptic; bark without a skunky odor; wet areas in South Dakota, NE Wyoming, Montana, & Idaho. ..... 26. *S. discolor.*
56. Twigs of previous year sometimes hairy; leaves, if present, obovate to oblanceolate; freshly stripped bark of living twigs of previous year usually with a skunky odor; widespread mostly in drier locations in upland forests and clearings. ..... 27. *S. scouleriana.*

KEY TO STAMINATE WILLOWS OF THE ROCKY MOUNTAIN STATES

1. Stamens 3–8 per flower. . . . . 2.
2. Bud scales with free overlapping margins. . . . . 3.
3. Leaf blades not glaucous beneath. . . . . 2. *S. gooddingii.*
3. Leaf blades glaucous beneath. . . . . 4.
4. Latest developing, expanded leaves lanceolate to ovate, with margins incurved just before tip, not coriaceous. 3. *S. amygdaloides.*
4. Latest developing, expanded leaves lanceolate with straight margins, somewhat coriaceous. . . . . 1. *S. bonplandiana.*
2. Bud scales without free overlapping margins. . . . . 5.
5. Plants introduced trees, not known to escape cultivation; leaves pale beneath but not glaucous. . . . . 4. *S. pentandra.*
5. Plants native shrubs, rarely tree-like; leaves green on both sides or glaucous beneath. . . . . 6.
6. Aments maturing in summer (July-August). . . . . 5. *S. serissima.*
6. Aments maturing in spring (March-June). . . . . 7.
7. Leaf blades mostly about 3 times as long as wide. . . . . 6. *S. lucida.*
7. Leaf blades mostly 4 or more times as long as wide. . . . . 7 & 7a. *S. lasiandra.*

1. Stamens 1 or 2 per flower. . . . . 8.
8. Anthers solitary. . . . . 46. *S. sitchensis.*
8. Anthers 2 per flower. . . . . 9.
9. Plants creeping, 1–8 cm high, near or above timberline. . . . . 10.
10. Leaves 7(–9) mm or less long, green on both sides. . . . . 16. *S. rotundifolia.*
10. Leaves, or some of them, over 7 mm long, whitish-glaucous beneath, except *S. cascadensis.* . . . . . 11.
11. Leaf tip usually rounded; leaves glaucous and prominently reticulate-veined beneath; flower bracts glabrous to short-hairy. . . . . 15. *S. reticulata.*
11. Leaf tip usually pointed; leaves glaucous or not beneath, usually not reticulate-veined; flower bracts mostly long-hairy. . . . 12.
12. Leaf blades mostly elliptic to oval, glaucous beneath, those of the previous year usually not persisting. 20. *S. arctica.*
12. Leaf blades narrowly elliptic to elliptic, usually equally green on both sides, those of the previous year often persisting. . . . . 21. *S. cascadensis.*

9. Plants mostly upright and mostly over 20 cm high, only rarely above timberline. . . . . 13.
13. Plants introduced trees. . . . . 14.
14. Branchlets very long and hanging straight downward. . . . . 10. *S. babylonica.*
14. Branchlets short or long, erect to ascending. . . . . 15.
15. Twigs brittle at base, easily broken off; leaves glabrous when expanded. . . . . 9. *S. fragilis.*

15. Twigs not brittle at base; leaves often pubescent. . . . . 8. *S. alba.*

13. Plants native shrubs, rarely tree-like. . . . . 16.

16. Twigs of previous year, and sometimes those of season, pruinose, sometimes only apparent at nodes, especially behind buds. . . . . 17.

17. Ments precocious, sessile or nearly so. . . . . 18.

18. Flower bracts mostly obovate or suborbicular, fringed with relatively short hairs. . . . . 31. *S. irrorata.*

18. Flower bracts mostly narrower, with very long hairs. . . . . 29. *S. drummondiana.*

17. Ments mostly coetaneous with at least short floriferous branchlets. . . . . 19.

19. Leaves sericeous and nearly the same color on both sides; flower bracts mostly brownish. 24. *S. geyeriana.*

19. Leaves sericeous on one side at most, obviously glaucous beneath; flower bracts mostly black. . . . . 25. *S. lemmonii.*

16. Twigs not pruinose (rarely so in *S. planifolia*). . . . . 20.

20. Twigs glutinous, staining pressing papers yellow or green. . . . . 47. *S. barrattiana.*

20. Twigs not glutinous. . . . . 21.

21. Ments, or some of them, at tips of twigs of previous year; twigs often with long, spreading hairs. . . . . 48. *S. tweedyi.*

21. Ments usually not at tips of twigs of previous year; twigs mostly without long, spreading hairs. . . . . 22.

22. Leaf blades elliptic-obovate to oval, dark green above, silvery-hairy beneath (becoming glabrate); ments at tips of ordinary shoots of season; Montana. . . . . 14. *S. vestita.*

22. Leaf blades not as above; ments usually at tips of modified shoots (on branchlets with no or reduced leaves). . . . . 23.

23. Ments mostly precocious, usually sessile or nearly so; flower bracts mostly black or dark brown, at least at tip. The following are difficult to distinguish using described characteristics. The most obvious tendencies are listed: 27. *S. scouleriana* — drier upland forests and clearings. 28. *S. planifolia* — twigs often chestnut or red and shiny; often subalpine. 42. *S. monticola* — early flowering; S Wyoming, Colorado, New Mexico, Arizona, Utah. 43. *S. lutea* — ments very slender and elongate; bracts often bicolored. 32. *S. lasiolepis* — bracts mostly suborbicular, fringed with short hairs; SW Idaho, S Utah, Nevada, Ari-

zona, New Mexico. 44. *S. ligulifolia* — plains and foothill streams; SE Wyoming, Colorado, New Mexico, Arizona, S Utah, Nevada. 25. *S. lemmonii* — aments loosely flowered. 33. *S. pseudomonticola* — early flowering; N Wyoming, South Dakota, Montana, Idaho. 26. *S. discolor* — very early flowering; South Dakota, NE Wyoming, Montana, Idaho.

23. Aments mostly coetaneous or serotinous, usually with at least short, leafy floriferous branchlets; flower bracts sometimes greenish, yellowish, or light brown. ..... 24.
24. Leaves densely white-tomentose beneath, greenish above. ..... 30. *S. candida.*
24. Leaves not white-tomentose except rarely so on both sides. .....
25. (Couplet moved to left margin of key.)

25. Leaves glaucous or glaucescent beneath. ..... 26.
26. Young leaves mostly glabrous. ..... 27.
27. Leaves somewhat leathery with rolled margins. ... 17. *S. pedicellaris.*
27. Leaves not leathery, the margins mostly flat. ..... 34. *S. farriae.*
26. Young leaves mostly pubescent. The following are difficult to distinguish using described characteristics. The most obvious tendencies are listed: 13. *S. melanopsis* — aments slender and elongate; bracts green or yellowish to tan. 22. *S. bebbiana* — margins of bud scales depressed; twigs of previous year reddish-purple, appressed-hairy. 43. *S. lutea* — aments slender and elongate; bracts bicolored. 42. *S. monticola* — early flowering; S Wyoming, Colorado, New Mexico, Arizona, Utah, mostly in mountains. 32. *S. lasiolepis* — bracts mostly suborbicular, fringed with short hairs; SW Idaho, S Utah, Nevada, Arizona, New Mexico. 44. *S. ligulifolia* — plains and foothill streams; SE Wyoming, Colorado, New Mexico, Arizona, S Utah, Nevada. 25. *S. lemmonii* — aments loosely flowered. 19. *S. glauca* — mostly subalpine; petioles mostly 3 mm or more long. 18. *S. brachycarpa* — petioles mostly 1–3 mm long; aments about twice as long as wide. 35. *S. barclayi* — mountains; NW Wyoming, Montana, Idaho. 38. *S. orestera* — extreme W Nevada. 23. *S. petiolaris* — aments loosely flowered; Montana, South Dakota, E Colorado.

25. Leaves not glaucous or glaucescent beneath. ..... 28.
28. Leaves linear or nearly so. ..... 29.
29. Leaf blades 0.5–3.5 cm long. ..... 11. *S. taxifolia.*
29. Leaf blades 2–13 cm long. ..... 12. *S. exigua.*
28. Leaves broader than linear. ..... 30.
30. Plants of Arizona. ..... 41. *S. arizonica.*
30. Plants not known from Arizona. ..... 31.
31. Leaves of floriferous branchlets usually with prominent glands on margins which stand out at a right angle. ..... 39. *S. eastwoodiae.*
31. Leaves of floriferous branchlets without glands as above. .... 32.
32. Leaves thin and somewhat translucent. 45. *S. monochroma.*

32. Leaves thickish, not translucent. ..... 33.
33. Leaves of floriferous branchlets little if at all reduced; leaf blades mostly ovate, broadly elliptic, or obovate, often densely pubescent with long, loose hairs. ..... 36. *S. commutata.*
33. Leaves of floriferous branchlets usually much reduced; leaf blades mostly lanceolate, narrowly elliptic, or oblanceolate, rarely broader, variously pubescent or glabrous. ..... 34.
34. Aments mostly less than 2 cm long; plants mostly less than 1(–2) m high. ..... 37. *S. wolfii.*
34. Aments mostly 2 cm or more long; plants often over 2 m high. ..... 35.
35. Plants of extreme west-central Nevada. ..... 38. *S. orestera.*
35. Plants widespread. ..... 40. *S. boothii.*

Salix Linnaeus, Gen. Pl. ed. 5. 447. 1754. TYPE SPECIES: *S. alba* L.

Subgenus **Salix**

I. Section *Humboldtianae* Pax in Engl. & Prantl, Nat. Pflanzenf. III, **1:** 36. 1887. TYPE SPECIES: *S. humboldtiana* Willd.

1. **Salix bonplandiana** HBK., Nov. Gen. & Sp. **2:** 24. 1817. TYPE: Syntypes from several localities in Mexico (P).

Salix laevigata Bebb, Am. Naturalist **8:** 202. 1874. TYPE: Syntypes from several localities in California (F).

Salix toumeyi Britt. in Britt. & Shafer, N. Am. Trees 187. 1908. TYPE: Sabino Canyon, Santa Catalina Mts., Pima Co., Arizona, *Shear 4201* (Lectotype by Schneider, 1918, NY).

Tree to 15 m high; leaf blades lanceolate or lance-linear or the younger oblanceolate, 2–15 cm long, acute or acuminate, entire or serrate, glaucous beneath, glabrous when mature; stamens 3–8; anthers 0.2–0.6 mm long; pistillate aments appearing at various times, 2–10 cm long, sessile or with leafy floriferous branchlets to 3 cm long; capsules glabrous; stipes 1–2.8 mm long; styles 0–0.4 mm long; bracts yellowish or greenish, pubescent, deciduous. $2n$ = 42(?).

Stream banks in Arizona, New Mexico, southern Nevada, and southern Utah. Additional distribution: California, Mexico, and Guatemala.

2. **Salix gooddingii** Ball, Bot. Gaz. **40:** 376. 1905. TYPE: Muddy

Creek, Clark Co., Nevada, *Goodding 689* (Holotype: US; isotype: RM!).

Shrub or tree to 30 m high; leaf blades linear-lanceolate or narrowly elliptic or oblong, 3–12 cm long, acuminate, serrate, green or pale beneath, glabrous when mature; stamens 3–8; anthers 0.3–0.6 mm long; pistillate aments appearing with the leaves, 2.5–7 cm long, with leafy floriferous branchlets 0.7–3 cm long; capsules glabrous or pubescent; stipes 1–2.5 mm long; styles 0–0.4 mm long; bracts yellowish, pubescent, deciduous. $2n = 38$.

Stream banks in Arizona, New Mexico, southern Utah, southern Nevada, and possibly southeast Colorado. Additional distribution: California, northern Mexico, and western Texas.

3. **Salix amygdaloides** Anderss., Proc. Am. Acad. Arts **4:** 53. 1858. TYPE: *Neuwied,* Ft. Pierre, South Dakota.

Tree to 17 m high, sometimes shrubby; leaf blades lanceolate or ovate, 4–12 cm long, long-acuminate at tip when expanded, glaucous or glaucescent beneath, serrate, glabrous except when young; stamens usually 5–8; anthers 0.3–0.6 mm long; pistillate aments appearing with the leaves, 2–10 cm long, with leafy floriferous branchlets (5)10–30(35) mm long; capsules glabrous; stipes 1.2–3 mm long; styles 0.5 mm or less long; bracts yellowish or white, pubescent, deciduous. $2n = 38$.

Flood plains, stream banks, and shores on the plains. Throughout the region. General distribution: British Columbia to Quebec south to northern Mexico, Missouri, Pennsylvania, and Massachusetts.

This species is often confused with *Salix lasiandra* but the difference in bud scales (see key) is absolute.

II. Section *Salicaster* Dumortier, Fl. Belg. 14. 1827. TYPE SPECIES: *S. pentandra* L.

4. **Salix pentandra** L., Sp. Pl. 1016. 1753. TYPE: None designated, *Europae paludibus montosis duris* cited.

Introduced tree to 20 m high; leaf blades ovate or broadly lanceolate or elliptic, 3–12 cm long, acuminate, serrate, pale but not glaucous beneath, glabrous; stamens usually 5; anthers 0.4–0.8 mm

long; pistillate aments appearing with or after the leaves, 2–6 cm long, with leafy floriferous branchlets 2–6 cm long; capsules glabrous; stipes 0.2–1.2 mm long; styles 0.2–0.7 mm long; bracts yellow or greenish, pubescent, deciduous. $2n = 57, 76$.

Sparingly planted. Native of Europe and western Asia.

5. **Salix serissima** (Bailey) Fernald, Rhodora **6:** 6. 1903.

Salix lucida var. *serissima* Bailey in Arthur et al., Bull. Geol. Nat. Hist. Surv. Minn. **3:** 19. 1887. TYPE: Mud River, Vermillion Lake, Minnesota, *Arthur, Bailey, & Holway B357* (Lectotype by Ball, 1921, F).

Shrub to 5 m high; leaf blades lanceolate or elliptic, 3–10 cm long, acute or acuminate, serrate, glaucescent or pale beneath, glabrous; stamens 3–8; anthers 0.4–0.7 mm long; pistillate aments appearing after the leaves, maturing in summer, 2–4 cm long, with leafy floriferous branchlets 1–4 cm long; capsules glabrous; stipes 0.8–2 mm long; styles 0.1–0.8 mm long; bracts yellow, green, or whitish, pubescent, deciduous.

Swamps and bogs. Very local in Montana, South Dakota, and Larimer Co., Colorado. General distribution: District of Mackenzie to Newfoundland south to Colorado, Indiana, and New Jersey.

This species is called the autumn willow because the aments mature in late summer or early fall. All the other Rocky Mountain, non-alpine willows have aments maturing in spring or early summer.

6. **Salix lucida** Muhl., Neue Schriften Ges. Berlin **4:** 239. 1803. TYPE: Lancaster, Pennsylvania, *Muhlenberg s.n.* (Holotype: PH!).

Shrub or tree to 6 m high; leaf blades lanceolate, lance-ovate, or elliptic, 3–15 cm long, acute or acuminate, serrate, pale beneath, glabrous except when young; stamens 3–8; anthers 0.5–0.9 mm long; pistillate aments appearing with the leaves, 2–7 cm long, with leafy floriferous branchlets 1–3 cm long; capsules glabrous; stipes 0.5–2 mm long; styles 0.3–0.8 mm long; bracts yellow or greenish, pubescent, deciduous. $2n = 76$.

Stream banks and swamps in South Dakota and extreme eastern Colorado. General distribution: Labrador to Saskatchewan south to Virginia and Colorado.

See discussion under 7a.

7. **Salix lasiandra** Benth., Pl. Hartw. 335. 1857. TYPE: Sacramento River, California, *Hartweg s. n.* (Holotype: K; isotype, GH!).

Salix fendleriana Anderss., Proc. Am. Acad. Arts **4:** 54. 1858. TYPE: New Mexico, *Fendler 816.*

Salix arguta Anderss., Kongl. Sv. Vet.-Akad. Handl. **6**(1): 32. 1867. TYPE: New Mexico, *Fendler 816.*

Shrub or small tree to 10 m high; leaf blades lanceolate to sometimes elliptic, usually acuminate when expanded, 2–15(20) cm long, toothed, glaucous beneath, glabrous; stamens 3–8; anthers 0.5–1 mm long; pistillate aments appearing with the leaves, 2–8 cm long, with leafy floriferous branchlets 10–45 mm long; capsules glabrous; stipes 0.8–2.2 mm long; styles 0.2–1 mm long; bracts yellowish, deciduous, pubescent to glabrate. $2n = 76$.

Stream banks in Arizona, New Mexico, Colorado, Utah, Nevada, Idaho, and northwest Montana. General distribution: Alaska to District of Mackenzie south to California and New Mexico.

7a. **Salix lasiandra** var. **caudata** (Nutt.) Sudw., Bull. Torrey Bot. Club **20:** 43. 1893.

Salix pentandra β caudata Nutt., N. Am. Sylva **1:** 61. 1842. TYPE: None designated, Rocky Mountains to Oregon cited.

Salix caudata (Nutt.) Heller, Muhlenbergia **2:** 186. 1906.

Differing from var. *lasiandra* in having the leaves not glaucous beneath. $2n = 76$.

Stream banks throughout the region. General distribution: British Columbia and Alberta south to California and New Mexico.

Salix lucida and the two varieties of *S. lasiandra* appear to have identical flavonoid profiles. More study is needed to determine the relationship between these taxa. The former appears to have leaves that are more acuminate at the tip. Leaf length with respect to width is not always a reliable character.

III. Section *Salix*. TYPE SPECIES: *S. alba* L.

8. **Salix alba** L., Sp. Pl. 1021. 1753. TYPE: None designated, *Europae* cited.

Introduced tree to 30 m high; branchlets not brittle; leaf blades lanceolate to elliptic, 3–15 cm long, acuminate, serrate, glaucous or

lighter beneath, pubescent at least when young; stamens 2; anthers 0.5–0.9 mm long; pistillate aments appearing with the leaves, 3–7 cm long, with leafy floriferous branchlets 1–4 cm long; capsules glabrous; stipes 0–1 mm long; styles 0.1–0.7 mm long; bracts yellow or greenish, pubescent, deciduous. $2n = 76$.

Sparingly planted. Native of Europe and western Asia.

Salix alba is known to hybridize with *S. fragilis*.

9. **Salix fragilis** L., Sp. Pl. 1017. 1753. TYPE: None designated, *Europae borealibus* cited.

Introduced tree to 20 m high; branchlets brittle at base; leaf blades lanceolate or narrowly elliptic, 3–17 cm long, acute or acuminate, serrate, glaucous or glaucescent beneath, glabrous when mature; stamens 2; anthers 0.5–1.2 mm long; pistillate aments appearing with the leaves, 2–8 cm long, with leafy floriferous branchlets 1–5 cm long; capsules glabrous; stipes 0.5–1 mm long; styles 0.3–0.8 mm long; bracts yellow or greenish, pubescent, deciduous. $2n = 38, 76, 114$.

Widely planted. Native of Europe and western Asia.

This is by far the most common introduced willow in the region, and it is known to hybridize with *Salix alba*.

10. **Salix babylonica** L., Sp. Pl. 1017. 1753. TYPE: None designated, *Oriente* cited.

Introduced tree to 12 m high; branchlets long and hanging downward; leaf blades linear-lanceolate, 3–12 cm long, acuminate, serrate, glaucous or glaucescent beneath, glabrous when mature; stamens 2; pistillate aments appearing with the leaves, 1–2.5 cm long, with leafy floriferous branchlets 2–15 mm long; capsules glabrous, sessile; styles lacking or to 0.5 mm long; bracts yellow or greenish, pubescent, deciduous. $2n = 76$.

Sparingly planted. Native of Asia. Weeping willow.

IV. Section *Longifoliae* Pax in Engl. & Prantl, Nat. Pflanzenf. III, **1:** 36. 1887. TYPE SPECIES: *S. exigua* Nutt.

11. **Salix taxifolia** HBK., Nov. Gen. & Sp. **2:** 22. 1817. TYPE: None designated, *Colitur in hortis Mexici, Queretari, Zelayae* cited (P).

Tree or shrub to 12 m high; leaf blades mostly linear, 5–35 mm long, acute or acuminate, entire or nearly so, green on both sides, pubescent; stamens 2; anthers 0.3–0.6 mm long; pistillate aments appearing with the leaves, 0.7–2 cm long, 1 to several terminating branchlets of season; capsules pubescent; stipes 0–0.5 mm long; styles 0–0.2 mm long; bracts yellowish, pubescent, deciduous.

Stream banks in southern Arizona and New Mexico. Additional distribution: southwest Texas, Mexico, Guatemala, and Puerto Rico.

12. **Salix exigua** Nutt., N. Am. Sylva **1:** 75. 1842. TYPE: Border of the Oregon a little below its confluence with the Wahlamet, *Nuttall.*

Salix longifolia Muhl., Neue Schriften Ges. Berlin **4:** 238. 1803, not Lam. in 1778. TYPE: Lancaster, Pennsylvania, *Muhlenberg s. n.* (Holotype, PH!).

Salix interior Rowlee, Bull. Torrey Bot. Club **27:** 253. 1900. Based on *S. longifolia* Muhl.

Salix argophylla Nutt., N. Am. Sylva **1:** 71. 1842. TYPE: River Boisée towards its junction with the Shoshonee [Snake], Idaho, *Nuttall.*

Salix fluviatilis of authors, not Nutt.

Salix nevadensis Wats., Am. Naturalist **7:** 302. 1873. TYPE: near Carson City, Nevada, *Watson 1093* (Lectotype by Schneider 1919b, GH).

Salix longifolia tenerrima Henderson, Bull. Torrey Bot. Club **27:** 354. 1900. TYPE: Elmore Co., Idaho, *Henderson* in 1895 (US).

Salix tenerrima (Henderson) Heller, Cat. N. Am. Pl. **2:** 4. 1900.

Salix stenophylla Rydb., Bull. Torrey Bot. Club **28:** 271. 1901. TYPE: Cuchara River below La Veta, Colorado, *Rydberg & Vreeland 6393* (NY).

Salix linearifolia Rydb. in Britt., Man. 316. 1901. TYPE: None designated, Minn. & Sask. to Indian Terr. & Colo. cited (NY).

Shrub to 5 m high; leaf blades linear to oblong, 2–13 cm long, entire or toothed, not glaucous, glabrous or pubescent; stamens 2; anthers 0.3–1.2 mm long; pistillate aments appearing with or after the leaves, 1.5–6 cm long, with usually leafy floriferous branchlets 5–25 mm long or at tips of long leafy branchlets; capsules glabrous or pubescent; stipes 0–1.5(2) mm long; styles to 0.2 mm long; bracts yellow or light brown, deciduous, pubescent or sometimes glabrate. $2n = 38$.

Stream banks, shores, and ditches throughout the region at mostly lower and middle elevations. General distribution: Alaska and Canada east to New Brunswick and south to northern Mexico, Mississippi, and Virginia.

This is the common narrow-leaved willow of the plains and

basins. The whole group is badly in need of detailed study which might well demonstrate the presence of more species than recognized here. The area of southern Idaho, eastern Oregon, and California is especially critical. A flavonoid survey of the group was inconclusive.

13. **Salix melanopsis** Nutt., N. Am. Sylva **1:** 78. 1842. TYPE: Fort Hall, Idaho, *Nuttall* in 1834.

Shrub to 5 m high; leaf blades linear or oblong, 2–12 cm long, toothed or subentire, usually glaucous or glaucescent beneath, glabrous, or pubescent when young; stamens 2; anthers 0.5–0.9 mm long; pistillate aments appearing with or after the leaves, 1.5–5 cm long, with usually leafy floriferous branchlets 3–20 mm long or at ends of long leafy branchlets; capsules glabrous or sometimes pubescent; stipes 0–0.5 mm long; styles 0–0.1 mm long; bracts yellow or greenish, glabrous to sometimes pubescent at base, deciduous.

Stream banks, mostly montane, in Montana, Wyoming, Colorado, Idaho, and reported from Utah and Nevada. Additional distribution: British Columbia, Alberta, Washington, Oregon, and California.

Subgenus **Vetrix** (Dumortier) Dumortier, Bull. Soc. Roy. Bot. Belg. **1:** 141. 1862. TYPE SPECIES: *S. caprea* L.

V. Section *Chamaetia* Dumortier, Bijdr. Natuurk. Wetensch. **1**(1): 56. 1825. TYPE SPECIES: *S. reticulata* L.

14. **Salix vestita** Pursh, Fl. Am. Sept. 610. 1814. TYPE: Labrador, Herb. Lambert & Banks.

Salix fernaldii Blank., Mont. Agr. Coll. Sci. Stud. Bot. **1:** 46. 1905. TYPE: mountains above Stanton Lake, Flathead Co., Montana, *Williams 1031* (pistillate) (Lectotype here designated, MONT!).

Shrub to 1 m high; leaf blades elliptic-obovate to oval, 1.5–7 cm long, rounded at tip, entire or with obscure glands on margins, glaucous and usually silvery-hairy beneath; stamens 2; anthers 0.2–0.5 mm long; pistillate aments appearing after the leaves, 1–5 cm long, terminating the branches on naked branchlets 5–20 mm long; capsules pubescent; stipes lacking or to 0.5 mm long; styles lacking or to 0.4 mm long; bracts brown or yellowish, pubescent, persistent.

$2n = 38$.

Subalpine in central (Big Snowy Mts.) and northwest Montana. General distribution: Labrador to District of Keewatin south to northern Manitoba and Newfoundland; southern British Columbia and Alberta, Montana, Washington, and northeast Oregon; central Asia.

15. **Salix reticulata** L., Sp. Pl. 1018. 1753, ssp. **nivalis** (Hook.) Löve et al., Arctic & Alp. Res. **3:** 146. 1971.

Salix nivalis Hook., Fl. Bor. Am. **2:** 152. 1838. TYPE: Rocky Mountains of southern Canada, *Drummond* (Holotype, K; fragment, A!).

Salix saximontana Rydb., Bull. N. Y. Bot. Gard. **1:** 261. 1899. TYPE: Gray's Peak, Colorado, *Rydberg* in 1895 (NY).

Salix aemulans von Seemen, Engl. Bot. Jahrb. **29**(65): 28. 1900. TYPE: Mt. Hesperus, Colorado, *Baker, Earle, & Tracy 299* (Isotype: GH!).

Creeping shrub to 8 cm high; leaf blades elliptic to obovate or suborbicular, (4)7–30 mm long, entire, glaucous beneath, glabrous or glabrate; stamens 2; anthers 0.3–0.7 mm long; pistillate aments appearing with or after the leaves, 5–20 mm long, with mostly naked floriferous branchlets 3–20 mm long; capsules pubescent; stipes 0.5 mm or less long; styles less than 0.5 mm long; bracts green, reddish, or yellowish, glabrous or glabrate, persistent. $2n = 38$.

Alpine or subalpine throughout the region except for Arizona and South Dakota. General distribution of the subspecies: Alberta and British Columbia south to California and New Mexico.

The extremes of *Salix reticulata* ssp. *reticulata* in Alaska and Canada and ssp. *nivalis* are strikingly distinct in the field, but plants are not infrequently encountered that would be hard to identify without knowing the locality. Specifically, I have seen plants in Colorado which resemble those in Alaska. The flavonoid profiles of the two subspecies appear to be identical and the chromosome numbers are the same. It is likely that the northern and southern populations were isolated during glaciation and have since come back together. On the basis of morphology, chromosome number, and flavonoid chemistry, I do not think that they have diverged sufficiently to be reproductively isolated, but this suspicion needs to be confirmed experimentally. *Salix* × *solheimii* Kelso is a hybrid between this subspecies and *S. rotundifolia* ssp. *dodgeana*.

VI. Section *Myrtosalix* Kerner, Verh. Zool.-Bot. Ges. Wien (Abhandl.) **10:** 203. 1860. TYPE SPECIES: *S. myrsinites* L.

16. **Salix rotundifolia** Trautv., Nouv. Mem. Soc. Nat. Mosc. **2:** 304. 1832, ssp. **dodgeana** (Rydb.) Argus, Canad. J. Bot. **47:** 795. 1969.

Salix dodgeana Rydb., Bull. N. Y. Bot. Gard. **1:** 277. 1899. TYPE: Electric Peak, Yellowstone Park, Montana, *Rydberg & Bessey s. n.* (Lectotype by Schneider 1919a, NY!).

Creeping, matted shrub to 3 cm high; leaf blades elliptic or ovate to suborbicular, 2–7(9) mm long, entire, not glaucous, glabrous except ciliate on margins; stamens 2; anthers 0.3–0.7 mm long; pistillate aments appearing with or after the leaves, 2–9 flowered, usually terminating branches; capsules glabrous; stipes 0–0.8 mm long; styles 0.2–1 mm long; bracts reddish or brownish, glabrous except on upper margins, persistent.

Alpine or subalpine, usually on limestone, in northwest Wyoming and western Montana. Additional distribution of the subspecies: District of Mackenzie, Yukon, Alaska, and northeast USSR.

Leaves of previous seasons tend to persist giving this species the appearance of a dense carpet. Most evidence thus far supports inclusion of this plant under the boreal *Salix rotundifolia*. Argus (1969) discussed its morphology. I have collected both subspecies, and the flavonoid profiles appear identical. This is not necessarily evidence for their being conspecific, however, since the profiles of *S. arctica* and *S. cascadensis* also appear identical. Our subspecies readily hybridizes with *S. reticulata* ssp. *nivalis* so the chromosome number may be $2n = 38$. My attempts to obtain a count were unsuccessful. Subspecies *rotundifolia* is $2n = 114$. All populations of ssp. *dodgeana* which I have seen are on limestone and most herbarium specimens from our region indicate the same habitat. I have not seen ssp. *dodgeana* in Canada or Alaska. Subspecies *rotundifolia* was not on limestone. More study is desirable.

VII. Section *Glaucae* Pax in Eng. & Prantl, Nat. Pflanzenf. III, **1:** 37. 1887. TYPE SPECIES: *S. glauca* L.

17. **Salix pedicellaris** Pursh, Fl. Am. Sept. 611. 1814. TYPE: Catskill Mountains, New York, *Pursh.*

Shrub to 12 dm high; leaf blades oblanceolate, oblong, or narrowly obovate, 1.5–6 cm long, obtuse or rounded at tip, rarely acute, entire, usually glaucous beneath, glabrous; stamens 2; anthers 0.2–0.6 mm long; pistillate aments appearing with the leaves, 1–3 cm long, with leafy floriferous branchlets 0.8–4 cm long; capsules glabrous; stipes 2–4 mm long; styles 0–0.4 mm long; bracts yellowish, brown, or reddish, glabrous or sparsely pubescent, persistent. $2n = 38, 57, 76$.

Bogs and swamps in northern Idaho. General distribution: southeast Yukon to Newfoundland south to Oregon, Iowa, and New Jersey.

The rounded, leathery-appearing, glabrous leaves are quite distinctive for recognizing this species.

18. **Salix brachycarpa** Nutt., N. Am. Sylva **1:** 69. 1842. TYPE: Beer Springs (Soda Springs), Idaho, *Nuttall s. n.* (Holotype, BM; isotype, GH!).

Shrub to 1.5 m high; leaf blades elliptic to elliptic-obovate or oblong, 0.5–4 cm long, usually pubescent, mostly lighter beneath, entire; stamens 2; anthers 0.2–0.6 mm long; pistillate aments appearing with the leaves, 0.5–2 cm long, usually with leafy floriferous branchlets 2–10 mm long; capsules pubescent; stipes less than 0.5 mm long; styles 0.1–1 mm long; bracts yellow or brown, pubescent, persistent. $2n = 38$.

Meadows, slopes, and bogs in or near the mountains in Montana, Wyoming, Idaho, Utah, and Colorado. Additional distribution: Alaska, Canada, Washington, Oregon, and California.

This species is treated in detail by Argus (1965). There seems to be some intergrading of this species with the next, but it may simply reflect a greater range of variability than would be desirable for easy identification.

19. **Salix glauca** L., Sp. Pl. 1019. 1753. TYPE: None designated, *Alpibus Lapponicis & Pyrenaicis* cited.

Salix pseudolapponum von Seemen, Engl. Bot. Jahrb. **29**(65): 28. 1900. TYPE: Mt. Hesperus, Colorado, *Baker, Earle, & Tracy 300½* (Isotypes, A! GH! RM!).

Salix wolfii var. *pseudolapponum* (von Seemen) Jones, Willow Fam. Gt. Plateau 17. 1908.

Salix glauca var. *pseudolapponum* (von Seemen) Kelso, Biol. Leafl. **34:** 10. 1946.
Salix wyomingensis Rydb., Bull. Torrey Bot, Club **28:** 271. 1901. TYPE: Big Horn Mountains, Wyoming, *Tweedy 3434* (Holotype, NY; isotype, RM!).
Salix pseudolapponum var. *subincurva* E. H. Kelso, Rhodora **36:** 195. 1934. TYPE: Rocky Mountain National Park, Colorado, *L. Kelso 3503.*
Salix glauca var. *subincurva* (E. H. Kelso) L. Kelso, Biol. Leafl. **34:** 10. 1946.
Salix pseudolapponum var. *kenosha* L. Kelso, Biol. Leafl. **25:** 3. 1944. TYPE: Kenosha Pass, Colorado, *L. & E. H. Kelso 534.*
Salix glauca var. *kenosha* (L. Kelso) L. Kelso, Biol. Leafl. **34:** 10. 1946.

Shrub to 1.5 m high; leaf blades mostly elliptic to elliptic-obovate, 1.5–7 cm long, entire or nearly so, usually glaucescent beneath, pubescent to sometimes glabrous; stamens 2; anthers 0.5–1 mm long; pistillate aments appearing with the leaves, (1.5)2–5 cm long, with leafy floriferous branchlets 5–25 mm long; capsules pubescent; stipes 0–1.5 mm long; styles 0.3–1.5 mm long; bracts brown or black, pubescent, persistent. $2n = 76–176$.

Alpine or subalpine in Montana, Wyoming, eastern Idaho, Colorado, northern New Mexico, and Utah. Additional distribution: Eurasia, Alaska, Canada, Greenland, and Iceland.

This species is treated in detail by Argus (1965). In the Rocky Mountains there appear to be two phases of this species (Argus recognizes only one), which may be the result of habitat differences. Taller, upright plants grow at subalpine, often somewhat sheltered locations. Semi-prostrate plants that are often difficult to distinguish from *Salix arctica* grow in more exposed, almost alpine situations. In the field, both phases appear different from plants of Alaska and northern Canada. The status of these populations is still difficult to determine as there is considerable variation within each.

20. **Salix arctica** Pallas, Fl. Ross. **1**(2)**:** 86. 1789. TYPE: northern Siberia, *Sujef.*

Salix petrophila Rydb., Bull. N. Y. Bot. Gard. **1:** 268. 1899. Based on *S. arctica* δ *petraea* Anderss. in DC., Prodr. **16**(2)**:** 287. 1868. TYPE: Rocky Mountains of Canada, *Bourgeau* in 1858 (K).
Salix caespitosa Kennedy, Muhlenbergia **7:** 135. 1912. TYPE: Mt. Rose, Washoe Co., Nevada, *Kennedy 1173.*

Creeping shrub to 8 cm high; leaf blades elliptic to oval or rarely obovate, 0.7–3 cm long, obtuse or sometimes acute at tip, usually glaucous beneath, entire, glabrous or not; stamens 2; anthers 0.4–1 mm long; pistillate aments appearing with or after the leaves, 1–5

cm long, on leafy floriferous branchlets 5–35 mm long; capsules pubescent; stipes 0.5 mm or less long; styles 0.5–2 mm long; bracts brown or black, pubescent, persistent. $2n$ = 76, 114, ca. 120.

Alpine or subalpine throughout the region except for Arizona and South Dakota. Additional distribution: Eurasia, Alaska, Canada, Greenland, Iceland, Washington, Oregon, and California.

The plants referred here form a very complex group which must be studied world-wide before the relationships can be understood. Rocky Mountain populations are fairly uniform when compared to populations around the world. Depauperate specimens of *Salix glauca* are often difficult to distinguish from *S. arctica.*

21. **Salix cascadensis** Cockerell, Muhlenbergia **3:** 9. 1907. Based on *S. tenera* Anderss. in DC., Prodr. **16**(2)**:** 288. 1868, not A. Br. ex Unger in 1850. TYPE: Cascade Mountains, 49°, *Lyall* in 1860 (Holotype, K; isotype, GH!).

Creeping shrub to 4 cm high; leaf blades mostly elliptic, 3–20 mm long, entire, glabrous except when very young; stamens 2; anthers 0.2–0.7 mm long; pistillate aments appearing with the leaves, 6–20 mm long, with leafy floriferous branchlets 2–20 mm long; capsules pubescent; stipes 0.5 mm or less long; styles 0.3–1.2 mm long; bracts brown or black, usually pubescent, persistent.

Alpine or subalpine in widely scattered localities of Wyoming, Utah, Montana, and reported from Colorado. Additional distribution: British Columbia and Washington.

The flavonoid profiles of *Salix arctica* and *S. cascadensis* from the Medicine Bow Mountains of southeast Wyoming appear identical. However, the two species grow side by side here with no evidence of hybridization.

VIII. Section *Vetrix* Dumortier, Bijdr. Natuurk. Wetensch. **1**(1): 55. 1825. TYPE SPECIES: *S. caprea* L.

22. **Salix bebbiana** Sarg., Gard. & Forest **8:** 463. 1895. Based on *S. rostrata* Richards. in Frankl., Narr. 1st Journ. 753. 1823, not Thuill. in 1799. TYPE: None designated, localities in Canada cited (K).

S. perrostrata Rydb. in Britt. & Rydb., Bull. N. Y. Bot. Gard. **2:** 163. 1901. TYPE: near Hermosa, Black Hills of South Dakota, *Rydberg 1018.*

Shrub or sometimes tree-like to 7 m high; leaf blades elliptic or elliptic-obovate, 1–7 cm long, usually glaucous and pubescent at least beneath, entire or rarely slightly toothed; stamens 2; anthers 0.4–0.8 mm long; pistillate aments appearing with the leaves, 1.5–6 cm long, subsessile or with leafy floriferous branchlets to 15 mm long; capsules pubescent; stipes mostly 2–5 mm long; styles 0.4 mm or less long; bracts brown or yellowish, usually pubescent, persistent. $2n = 38$.

Woods, meadows, and swamps throughout the region. General distribution: Eurasia; Alaska and Canada south to California, New Mexico, Indiana, and New Jersey.

This is a very common species readily recognized by the reddish-purple, appressed-hairy branchlets and bud scales with depressed margins.

23. **Salix petiolaris** Smith, Trans. Linn. Soc. London **6:** 122. 1802.
TYPE: reputedly from Britain but cultivated from America, *Dickson.*

Shrub to 7 m high; leaf blades narrowly lanceolate, oblanceolate, or elliptic, 2–10 cm long, acute or acuminate, serrate to subentire, glaucous beneath, glabrous when mature; stamens 2; anthers 0.5–0.8 mm long; pistillate aments appearing with the leaves, 1–3.5 cm long, subsessile or with leafy floriferous branchlets to 2 cm long; capsules usually thinly pubescent; stipes 1–4 mm long; styles 0.1–0.3 mm long; bracts brown, pubescent, persistent. $2n = 38$.

Meadows, shores, and stream banks. Very local in South Dakota, Colorado, and reported from Montana. General distribution: New Brunswick to Alberta south to New Jersey and Colorado; outliers in Oklahoma, Virginia, and Georgia.

24. **Salix geyeriana** Anderss., Proc. Am. Acad. Arts **4:** 63. 1858.
TYPE: Coeur d'Aleine River, Idaho [Geyer, London Jour. Bot. **5:** 289, 1846] *Geyer 286* (Holotype, K; fragment A!).

Salix macrocarpa Nutt., N. Am. Sylva **1:** 67. 1842, not Ledeb. ex Trautv. in 1832.
TYPE: *Nuttall,* Oregon?

Shrub to 7 m high; twigs usually pruinose; leaf blades elliptic or nearly so, 1–8 cm long, entire or nearly so, often lighter beneath, usually pubescent; stamens 2; anthers 0.3–0.7 mm long; pistillate aments appearing with the leaves, 8–20(25) mm long,

with usually leafy floriferous branchlets 2–12(18) mm long; capsules pubescent; stipes 1–3 mm long; styles less than 0.8 mm long; bracts yellow or brown to sometimes black, pubescent, persistent. $2n = 38$.

Wet places throughout the region except New Mexico. General distribution: southern British Columbia and Montana south to California, Colorado, and western Nebraska.

Salix geyeriana usually has white-sericeous leaves which are obscurely glaucous. The bracts are often light in color and somewhat narrow. The leaves of *S. lemmonii* are usually distinctly glaucous beneath with few hairs, some of which are red. The bracts are usually black and broader. However, I have not been able to find a combination of morphological characteristics that will always separate the two species. The flavonoid profiles of the two species are distinctly different. The type of *S. geyeriana* may be what is now called *S. lemmonii*. Further study is needed.

25. **Salix lemmonii** Bebb in Wats., Bot. Calif. **2:** 88. 1879. TYPE: Sierra Co., California, *Lemmon s. n.* (Lectotype by Schneider 1920c, F; isolectotype, GH!).

Shrub to 5 m high; branchlets often pruinose; leaf blades oblanceolate or elliptic, 2–10 cm long, acute or acuminate, entire or rarely serrulate, glaucescent or glaucous beneath, glabrous or puberulent; stamens 2; anthers 0.4–0.7 mm long; pistillate aments appearing with or sometimes before the leaves, 1–4 cm long, subsessile or with leafy floriferous branchlets to 1 cm long; capsules pubescent; stipes 0.5–2 mm long; styles 0.2–0.7 mm long; bracts brown or black, pubescent, persistent. $2n$ = ca. 76.

Stream banks and wet meadows in Idaho, Montana, Wyoming, Colorado, and Nevada. Additional distribution: California and Oregon.

See discussion under *Salix geyeriana*.

26. **Salix discolor** Muhl., Neue Schriften Ges. Berlin **4:** 234. 1803. TYPE: Lancaster, Pennsylvania, *Muhlenberg s. n.* (Holotype, PH!).

Shrub to 7 m high; leaf blades mostly elliptic or oblanceolate, 3–12 cm long, usually somewhat wavy-toothed, glaucous beneath, glabrous, or pubescent beneath with often reddish hairs; stamens

2; anthers 0.5–0.9 mm long; pistillate aments appearing before the leaves, 2–7 cm long, sessile or nearly so; capsules pubescent; stipes 1–3 mm long; styles 0.3–1.2 mm long; bracts dark brown or black, pubescent, persistent. $2n = 76, 114$.

Wet places in widely scattered localities of South Dakota, northeast Wyoming, Montana, and Idaho. General distribution: Newfoundland to British Columbia south to Delaware, Missouri, and Idaho.

27. **Salix scouleriana** Barratt ex Hook., Fl. Bor. Am. **2:** 145. 1838. TYPE: Columbia River, *Scouler* in 1825 (Holotype, K; fragment A!).

Salix flavescens Nutt., N. Am. Sylva **1:** 65. 1842, not Host in 1828. TYPE: Rocky Mountains, *Nuttall s. n.* (Isotype, GH!).

Salix nuttallii Sarg., Gard. & Forest **8:** 463. 1895. Based on *S. flavescens* Nutt.

Shrub or tree to 15 m high; leaf blades mostly obovate or oblanceolate, 2–10 cm long, entire or sometimes toothed, glaucous beneath, glabrous or pubescent beneath; stamens 2; anthers 0.7–1.1 mm long; pistillate aments appearing before or sometimes with the leaves, 1.5–7 cm long, sessile or with floriferous branchlets to 13 mm long; capsules pubescent; stipes 0.8–2.8 mm long; styles 0.2–1.1 mm long; bracts dark brown or black, pubescent, persistent. $2n = 76$.

Woods, clearings, or occasionally on shores throughout the region. General distribution: Alaska to District of Mackenzie (Manitoba?) south to California and New Mexico.

This species is common in drier upland habitats and is readily recognized by the obovate to oblanceolate leaves. The flavonoid profile of the species appears identical to that of *Salix humilis* Marsh. Further study might show that rearrangements are necessary in this group.

IX. Section *Vimen* Dumortier, Bijdr. Natuurk. Wetensch. **1**(1): 56. 1825. TYPE: *S. viminalis* L.

28. **Salix planifolia** Pursh, Fl. Am. Sept. 611. 1814. TYPE: None designated, description from Labrador plants in garden of George Anderson.

Salix nelsonii Ball, Bot. Gaz. **40:** 379. 1905. TYPE: Laramie Peak, Albany Co., Wyoming, *Nelson 7580* (Holotype, US; isotype, RM!).

Shrub to 5 m high; leaf blades mostly elliptic, 1–8 cm long, entire or sometimes toothed, glaucous beneath, glabrous or slightly pubescent beneath; stamens 2; anthers 0.5–1 mm long; pistillate aments appearing before or sometimes with the leaves, 1.5–6 cm long, sessile or subsessile; capsules pubescent; stipes 0–1 mm long; styles 0.4–1.5 mm long; bracts black or sometimes brown, pubescent, persistent. $2n = 57, 76, 152$.

Mostly subalpine in wet places but occasional in the lower mountains in Idaho, Montana, Wyoming, South Dakota, Colorado, Utah, northern New Mexico, and northeast Nevada. General distribution of subspecies *planifolia:* Yukon to Labrador south to California, New Mexico, northern Minnesota, and New Hampshire.

The branchlets of this species are often bright red.

29. **Salix drummondiana** Barratt ex Hook., Fl. Bor. Am. **2:** 144. 1838. TYPE: Rocky Mountains of Canada, *Drummond 672* (Lectotype by Argus 1973, K; fragment A).

Salix pachnophora Rydb., Bull. Torrey Bot. Club **31:** 403. 1904. TYPE: Chambers Lake, Colorado, *Agr. Coll. of Colorado* in 1899 (NY).

Shrub to 6 m high; twigs usually pruinose; leaf blades elliptic, oblong, or oblanceolate, rarely obovate, 1.5–11 cm long, entire or nearly so, silvery-hairy beneath, green and glabrous or glabrate above; stamens 2; anthers 0.3–0.6 mm long; pistillate aments appearing before or with the leaves, 1.5–6 cm long, sessile or nearly so; capsules pubescent; stipes 0.1–0.8 mm long; styles 0.5–1.8 mm long; bracts brown or black, pubescent, persistent. $2n = 38, 57, 76$.

Stream banks and swamps mostly in the mountains throughout the region except Arizona. General distribution: southeast Yukon to Saskatchewan south to California and New Mexico.

My chromosome count of $2n = 38$ is for a plant with oblong-lanceolate leaves that are densely silver-pubescent beneath. My counts of $2n = 76$ are from plants with broader leaves that are less pubescent beneath. These forms may represent different species. The former matches the description of the lectotype of *Salix*

drummondiana. The latter may correspond to *S. pachnophora.* The flavonoid profiles of the two forms appear identical, yet more study is needed. This species is often confused with *S. geyeriana* and *S. lemmonii,* but the closely flowered pistillate aments and silvery-pubescent lower leaf surface readily distinguish it from the two species which have loosely flowered aments.

30. **Salix candida** Flügge ex Willd., Sp. Pl. **4:** 708. 1806. TYPE: none designated, specimen from Willdenow Herbarium seen on microfiche.

Shrub to 1.5 m high; leaf blades elliptic or oblong or sometimes oblanceolate, 1–9 cm long, white-tomentose beneath, less pubescent or glabrate above, entire or nearly so; stamens 2; anthers 0.3–0.6 mm long; pistillate aments appearing before or with the leaves, 1–6 cm long, sessile or with leafy floriferous branchlets to 9 mm long; capsules pubescent; stipes less than 1 mm long; styles 0.2–1.7 mm long; bracts brown or yellowish, rarely black, pubescent, persistent. $2n = 38$.

Bogs. Very local in Fremont Co., Idaho, Montana, Wyoming, South Dakota, and northern Colorado. General distribution: Alaska and Canada south to northern Colorado, Iowa, and New Jersey.

This species is easily recognized by the densely white-tomentose lower leaf surface.

X. Section *Brewerianae* Schneider, Jour. Arnold Arb. **1:** 95. 1919. TYPE SPECIES: *S. breweri* Bebb.

31. **Salix irrorata** Anderss., Proc. Am. Acad. Arts **4:** 57. 1858. TYPE: Santa Fe, New Mexico, *Fendler 812.*

Shrub to 5 m high; branchlets usually pruinose; leaf blades oblong-elliptic or oblanceolate, 2–10 cm long, acute or obtuse at tip, entire or obscurely toothed, glaucescent beneath, glabrous when mature; stamens 2; anthers 0.4–0.6 mm long; pistillate aments usually appearing before the leaves, 2–4 cm long, sessile or nearly so; capsules glabrous; stipes 0.3–1 mm long; styles 0.2–0.7 mm long; bracts brown or black, pubescent, persistent.

Stream banks in Colorado, New Mexico, and Arizona. Additional distribution: southwest Texas.

32. **Salix lasiolepis** Benth., Pl. Hartw. 335. 1857. TYPE: near Monterey, California, *Hartweg s. n.* (Holotype, K; isotype, GH!).

Salix boiseana A. Nels., Bot. Gaz. **54:** 406. 1912. TYPE: near Boise, Idaho, *Clark 48* (Holotype, RM!).

Salix sandbergii Rydb., Bull. Torrey Bot. Club **39:** 304. 1912. TYPE: Valley of Hatwai Creek, Idaho, *Sandberg, MacDougal, & Heller 71* (Holotype, NY; isotypes, A! GH!).

Shrub or tree to 12 m high; leaf blades oblanceolate or oblong or sometimes obovate, 2–12 cm long, acute to obtuse at tip, entire or nearly so, glaucous beneath, pubescent or glabrous; stamens 2; anthers 0.4–0.8 mm long; pistillate aments appearing before or with the leaves, 2–6 cm long, subsessile; capsules glabrous; stipes 0.5–2 mm long; styles 0.1–0.6 mm long; bracts black or brown, pubescent, persistent. $2n = 38$.

Stream banks in southwest Idaho, Nevada, Arizona, southern Utah, and New Mexico. Additional distribution: southern Washington, Oregon, California, southwest Texas, and northern Mexico.

XI. Section *Cordatae* Barratt ex Hook., Fl. Bor. Am. **2:** 149. 1838. TYPE SPECIES: *S. rigida* Muhl.

Many species of this section are treated in more detail elsewhere (Dorn, 1975a). The 13 species treated here all have different flavonoid profiles. Compounds were identified for eight of the 13 species. Three polyploid levels are known in the section.

33. **Salix pseudomonticola** Ball in Standley, Contr. U. S. Natl. Herb. **22:** 321. 1921. TYPE: Rocky Mountains Park, Alberta, *Sanson 233* (Lectotype by Ball, 1923, US!).

Salix barclayi var. *pseudomonticola* (Ball) Kelso, Biol. Leafl. **34:** 8. 1946.

Shrub to 6 m high; leaf blades elliptic to ovate or obovate, 2.5–10 cm long, crenate-serrate, glaucous beneath, glabrous except when young, the young usually reddish; stamens 2; anthers 0.4–0.6 mm long; pistillate aments usually appearing before the leaves, 1–9 cm long, sessile or with sometimes leafy floriferous branchlets to 7(12) mm long; capsules glabrous; stipes 0.5–2.5(3) mm long;

styles (0.5)0.7–1.8 mm long; bracts brown or black, pubescent, persistent. $2n = 38$.

Stream banks, swamps, and wet meadows in the mountains of eastern Idaho, Montana, northern Wyoming, and South Dakota. Additional distribution: Alaska and Canada east to northwest Quebec.

This species is best recognized by the sessile or subsessile precocious aments with glabrous pistils and the reddish young leaves.

34. **Salix farriae** Ball in Standley, Contr. U. S. Natl. Herb. **22:** 321. 1921. TYPE: Field, British Columbia, *Farr 558* (Lectotype by Ball, 1934, US!).

Salix hastata var. *farriae* (Ball) Hultén, Ark. Bot. 7(1): 42. 1968.

Salix farriae var. *microserrulata* Ball, Univ. Calif. Publ. Bot. **17:** 410. 1934. TYPE: near Banff, Alberta, *Malte & Watson 898* (Holotype, US!).

Shrub to 1.5(2) m high; leaf blades elliptic to elliptic-obovate, 2–7 cm long, entire or occasionally serrulate, glaucous beneath, glabrous; stamens 2; anthers 0.3–0.6 mm long; pistillate aments appearing with the leaves, 1–4.5 cm long, with leafy floriferous branchlets (3)5–15 mm long; capsules glabrous; stipes 0.3–1.5(2) mm long; styles 0.3–1.2 mm long; bracts yellow or green to brown or black, pubescent to glabrous, persistent.

Meadows and stream banks in the mountains of Idaho, Montana, and northwest Wyoming. Additional distribution: Alberta, British Columbia, and northeast Oregon.

This species is best recognized by the usually entire, glabrous, pale green leaves with a distinctive venation on the glaucous surface.

35. **Salix barclayi** Anderss., Proc. Am. Acad. Arts **4:** 66. 1858. TYPE: Kodiak Island, Alaska, *Barclay s. n.* (Holotype, K!).

Salix conjuncta Bebb, Bot. Gaz. **13:** 111. 1888. TYPE: Mt. Adams, Washington, *Parry* in 1880 (Lectotype by Dorn, 1975a, F!).

Salix barclayi var. *conjuncta* (Bebb) Ball ex Schneider, Jour. Arnold Arb. **1:** 151. 1920: **3:** 73. 1922.

Shrub to 2 m high; leaf blades ovate-elliptic or narrowly elliptic to obovate, 2.5–9 cm long, serrate or rarely entire, glaucous beneath, often pubescent above especially when young; stamens 2; anthers 0.5–1 mm long; pistillate aments appearing with the leaves,

1–6 cm long, with leafy floriferous branchlets (0.5)1–3 cm long; capsules glabrous; stipes 0.5–1.5(2) mm long; styles (0.5)0.7–2.5 mm long; bracts brown or black, pubescent, persistent. $2n = 76$.

Mountain slopes, stream banks, and swamps in northwest Wyoming, Montana, and Idaho. General distribution: Alaska to District of Mackenzie south to Washington and northwest Wyoming.

36. **Salix commutata** Bebb, Bot. Gaz. **13:** 110. 1888. TYPE: Eagle Creek Mts., Oregon, *Cusick 826* (Lectotype by Dorn, 1975a, F!).

Salix barclayi var. *commutata* (Bebb) Kelso, Biol. Leafl. **34:** 8. 1946.

Salix commutata var. *sericea* Bebb, Bot. Gaz. **13:** 111. 1888. TYPE: Mt. Hood, Oregon, *Howell s. n.* (Lectotype by Dorn, 1975a, F!).

Salix commutata var. *mixta* Piper, Contr. U. S. Natl. Herb. **11:** 216. 1906. Based on *S. commutata* var. *sericea* Bebb.

Salix commutata var. *denudata* Bebb, Bot. Gaz. **13:** 111. 1888. TYPE: Eagle Creek Meadows, Oregon, *Cusick 968* (Lectotype by Dorn, 1975a, F!).

Salix commutata var. *puberula* Bebb, Bot. Gaz. **13:** 111. 1888. TYPE: Oregon, *Cusick* sheet 7745 (Lectotype by Dorn, 1975a, F!).

Shrub to 3 m high; leaf blades elliptic or oval to ovate or obovate, the larger (1)3–7(9) cm long, (0.5)1.5–3(4) cm wide, entire or glandular-toothed, not glaucous, densely pubescent with long hairs when young, often becoming glabrate later; stamens 2; anthers 0.4–1 mm long; pistillate aments appearing with the leaves, (2)3–7(10) cm long including the floriferous branchlet, the latter 8–30 mm long and leafy; capsules glabrous or rarely puberulent; stipes (0.3)0.8–2 mm long; styles 0.5–1.5 mm long; bracts light brown or yellowish to black, pubescent, persistent. $2n = 38$.

Moist meadows and stream banks, usually subalpine, in Idaho and western Montana. General distribution: Alaska to District of Mackenzie south to northern Oregon and western Montana.

37. **Salix wolfii** Bebb in Rothr., Bot. Wheeler Exp. 241. 1878. TYPE: South Park, Colorado, *Wolf & Rothrock 820* (Lectotype by Schneider, 1920b, F; isolectotype, GH!).

Salix wolfii var. *idahoensis* Ball, Bot. Gaz. **40:** 378. 1905. TYPE: Forks of Wood River, Idaho, *Henderson 3399* (US).

Salix idahoensis (Ball) Rydb., Fl. Rocky Mts. 197, 1061. 1917.

Shrub to 2 m high; leaf blades mostly elliptic, lanceolate, or oblanceolate, 1–6 cm long, entire, not glaucous, pubescent; stamens 2; anthers 0.3–0.7 mm long; pistillate aments appearing with

the leaves, 8–20 mm long, subsessile or with leafy floriferous branchlets to 12 mm long; capsules glabrous or pubescent; stipes 0–0.8 mm long; styles 0.2–1.3 mm long; bracts brown or black, pubescent, persistent. $2n = 38$.

Wet places in the mountains of Colorado, Utah, Nevada, Wyoming, Idaho, and southern and central Montana. Additional distribution: northeast Oregon.

This species is normally less than 1 meter high but occasionally reaches 2 meters. The short aments and sericeous leaves are distinctive.

38. **Salix orestera** Schneider, Jour. Arnold Arb. **1:** 164. 1920. TYPE: Mt. Goddard, Fresno Co., California, *Hall & Chandler 695* (Isotype, NY!).

Salix glauca ssp. *orestera* (Schneider) Youngb., Madroño **21:** 124. 1971.

Shrub to 3 m high; leaf blades oblanceolate or elliptic, 2–8 cm long, acute, entire, glaucescent beneath or sometimes green on both sides, pubescent; stamens 2; anthers 0.6–1.1 mm long; pistillate aments appearing with the leaves, 1–4 cm long, with leafy floriferous branchlets 3–15(25) mm long; capsules pubescent; stipes 0.5–2 mm long; styles 0.5–1.5 mm long; bracts brown or black, pubescent, persistent.

Stream banks and wet meadows in the mountains of western Nevada. Additional distribution: California.

39. **Salix eastwoodiae** Cockerell ex Heller, Cat. N. Am. Pl. **3:** 89. 1910. Based on *S. californica* Bebb in Wats., Bot. Calif. **2:** 89. 1879, not Lesq. in 1878. TYPE: Sierra Nevada, California, *Lemmon s. n.* (Lectotype by Schneider 1920a, F!).

Salix commutata var. *rubicunda* Jepson, Man. Fl. Pl. Calif. 267. 1923. TYPE: Head of Lost Creek, Sawtooth Range, Tulare Co., California, *Jepson 4992* (Holotype, JEPS; isotype, A!).

Shrub to 4 m high; leaf blades lanceolate to elliptic or oblanceolate, rarely broader, 2–6(10) cm long, the margins prominently glandular at least when young, not glaucous, pubescent at least when young; stamens 2; anthers 0.3–1 mm long; pistillate aments appearing with or slightly before the leaves, 1–5 cm long, with leafy floriferous branchlets 3–12(20) mm long; capsules pubescent;

stipes 0.2–1.8 mm long; styles 0.4–1.5 mm long; bracts brown or black, pubescent, persistent. $2n$ = ca. 76.

Wet meadows and stream banks well up in the mountains of western Nevada, Idaho, western Wyoming, and southwest Montana. Additional distribution: California and Oregon.

The glands on the margins of young leaves or on leaves of floriferous branchlets are distinctive by being largely set out from the margin and oriented at a right angle to the margin. They are often rather crowded.

40. **Salix boothii** Dorn, Can. Jour. Bot. **53:** 1505. 1975. TYPE: Tributary to Pacific Creek, Teton Co., Wyoming, *Dorn 1288* (Holotype, RM!).

Salix myrtillifolia of authors, not Anderss.

Salix pseudomyrsinites of authors, not Anderss.

Salix curtiflora of authors, not Anderss.

Salix myrtillifolia var. *curtiflora* (Anderss.) Bebb ex Rose, Contr. U. S. Natl. Herb. **3:** 573. 1896. Misapplied.

Salix novae-angliae of authors, not Anderss.

Salix pseudocordata (Anderss.) Rydb., Fl. Colorado 94. 1906. Misapplied.

Salix novae-angliae l. *S. pseudo-myrsinites* (Anderss.) Anderss. c. *aequalis* Anderss., Kongl. Svenska Vetenskapsakad. Handl. **6**(1): 161. 1867. TYPE: Rocky Mountains of Alberta, *Bourgeau s. n.* (Holotype, K!).

Salix pseudomyrsinites var. *aequalis* (Anderss.) Anderss. ex Ball in Coult. & Nels., New Man. Rocky Mts. 133. 1909.

Salix pseudocordata var. *aequalis* (Anderss.) Ball ex Schneider, Jour. Arnold Arb. **2:** 196; **3:** 73. 1922.

Shrub to 6 m high; leaf blades lanceolate to elliptic or oblanceolate or rarely lance-ovate, the larger (1)2–8(10) cm long, (0.4)0.8–2.5 cm wide, serrate to entire, not glaucous, pubescent at least when young, often becoming glabrous; stamens 2; anthers 0.3–0.7 mm long; pistillate aments appearing with or slightly before the leaves, (1)2–5 cm long, the floriferous branchlets (1)2–10(15) mm long and usually leafy; capsules glabrous; stipes 0.5–2(2.5) mm long; styles 0.3–1.2(1.5) mm long; bracts brown to black, pubescent or rarely glabrous, persistent. $2n$ = 76.

Stream banks and swamps from sagebrush plains near the mountains to near subalpine in Idaho, Montana, Wyoming, Colorado, Nevada, and Utah. Additional distribution: northeast California, northeast Oregon, southern British Columbia, and southern Alberta.

41. **Salix arizonica** Dorn, Can. Jour. Bot. **53:** 1499. 1975. TYPE: T7N, R27E NW¼ Sec 18, 9100 ft., Apache Co., Arizona, *Granfelt 69–191* (Holotype, ARIZ!).

Shrub at least 0.5 m high; leaves ovate, broadly elliptic, or obovate, 1–4.5 cm long, 5–22 mm wide, serrulate, not glaucous, glabrous or nearly so or the younger pubescent; stamens 2; anthers 0.3–0.6 mm long; pistillate aments appearing with or slightly before the leaves, 1–4 cm long, the floriferous branchlets 3–12 mm long and leafy; capsules glabrous; stipes 0.2–1.5 mm long; styles 0.6–1.5 mm long; bracts brown to rarely black, pubescent, persistent.

Wet meadows and stream banks. Endemic in the White Mountains of Arizona.

All known collections of this species are within 10 miles of each other.

42. **Salix monticola** Bebb in Coult., Man. Rocky Mt. Reg. 336. 1885. TYPE: near Golden, Colorado, *Greene 8* (Lectotype by Dorn 1975a, F!).

Salix cordata var. *monticola* (Bebb) Kelso, Biol. Leafl. **34:** 7. 1946.

Salix padifolia Rydb., Bull. Torrey Bot. Club **28:** 272. 1901, not Anderss. in 1858. TYPE: Tributaries of Turkey Creek, Colorado, *Rydberg & Vreeland 6389* (Holotype, NY!).

Salix padophylla Rydb., Bull. Torrey Bot. Club **28:** 499. 1901. Based on *S. padifolia* Rydb.

Salix pseudomonticola var. *padophylla* (Rydb.) Ball, Jour. Wash. Acad. Sci. **28:** 450. 1938.

Salix barclayi var. *padophylla* (Rydb.) Kelso, Biol. Leafl. **34:** 8. 1946.

Salix barclayi var. *veritomonticola* Kelso, Biol. Leafl. **34:** 8. 1946. TYPE: Leadville, Colorado, *Kelso 6173* (Neotype by Dorn 1975a, RM!).

Salix barclayi var. *cochetopiana* Kelso, Biol. Leafl. **34:** 8. 1946. TYPE: Leadville, Colorado, *L. & E. H. Kelso 5575* (Neotype by Dorn 1975a, RM!).

Salix sawatchicola Kelso, Biol. Leafl. **34:** 9. 1946. TYPE: Leadville, Colorado, *Kelso 4872* (Holotype, RM!).

Salix amelanchieroides Kelso, Biol. Leafl. **34:** 9. 1946. TYPE: Leadville, Colorado, *Kelso 5419* (Holotype, GH!).

Salix barclayi var. *resurrectionis* Kelso, Biol. Leafl. **36:** 2. 1947. TYPE: Leadville, Colorado, *Kelso 5519* (Holotype, RM!).

Salix barclayi var. *uncompahgre* Kelso, Biol. Leafl. **37:** 4. 1947. TYPE: Sneffels Creek, Ouray, Colorado, *Kelso 5673* (Holotype, RM!).

Salix dissymmetrica Kelso, Biol. Leafl. **61:** 3. 1952. TYPE: Leadville, Colorado, *Kelso 6426* (Holotype, CAN!).

Shrub to 5 m high; leaf blades ovate to obovate, 2–8 cm long, crenate or serrate, rarely subentire, glaucous beneath, glabrous, or pubescent when young; stamens 2; anthers 0.4–0.9 mm long; pistillate aments appearing before or with the leaves, 1–6 cm long, subsessile or with leafy floriferous branchlets to 8(17) mm long; capsules usually glabrous; stipes 0.3–1.5(2) mm long; styles 0.7–1.8 mm long; bracts brown or black, pubescent, persistent. $2n = 114$.

Stream banks and wet meadows from the plains near the mountains to subalpine. Known only from southern Wyoming, Colorado, Utah, Arizona, and New Mexico.

43. **Salix lutea** Nutt., N. Am. Sylva **1:** 63. 1842. TYPE: Rocky Mountains to banks of the Oregon, *Nuttall.*

Salix flava Rydb., Bull. Torrey Bot. Club **28:** 273. 1901, not Gmel. in 1791. TYPE: Green River, Wyoming, *Rydberg* in 1895 (NY).

Salix cordata var. *watsonii* Bebb in Wats., Bot. Calif. **2:** 86. 1879. TYPE: Syntypes from Nevada and California (F).

Salix watsonii (Bebb) Rydb., Bull. Torrey Bot. Club **33:** 137. 1906.

Shrub to 6 m high; leaf blades mostly lanceolate or nearly so, 1.5–11 cm long, toothed or sometimes entire, glaucous beneath, glabrous except when young; stamens 2; anthers 0.4–0.8 mm long; pistillate aments appearing before or with the leaves, 2–6 cm long, sessile or with leafy floriferous branchlets to 15 mm long; capsules glabrous; stipes (1)2–4.5 mm long; styles 0.2–0.7(0.8) mm long; bracts brown or black, usually glabrous or glabrate, persistent. $2n = 38$.

Wet places throughout the region except possibly not in Arizona or New Mexico. General distribution: Washington and Alberta to Manitoba south to California and at least to Nebraska and Colorado.

A distinguishing feature for this species is the silvery-gray bark on the older twigs. The staminate aments are also distinctive in appearance, but they are difficult to describe. The species was recently considered to be conspecific with *Salix rigida* Muhl., but the two differ in morphology, distribution, and flavonoid chemistry. The flavonoid profiles indicate that *S. rigida* and *S. cordata* Michx. have flavones and flavonols in the leaves while *S. lutea*

and the other related western species probably have only flavonols. *Salix ligulifolia*, *S. mackenzieana*, and *S. monochroma* apparently also have distinct profiles but these are not as obviously different as those between the eastern and western plants. I am uncertain of the geographical limits of these species, and there may be more species than those recognized here. I have not been able to confirm the presence of *S. mackenzieana* in our region. The plants from Idaho south to Arizona and west to the coast are especially confusing. *Salix ormsbyensis* von Seemen is either a hybrid between *S. lutea* and *S. ligulifolia* or the same as the latter species. The group is extremely complex and the problems cannot be resolved without extensive study. In general, *S. ligulifolia* has short stipes and bluish-green leaves, *S. monochroma* has non-glaucous and thin leaves, *S. lutea* has a silvery-gray bark on the older twigs, and *S. mackenzieana* has very long stipes. These are the most apparent morphological characteristics for recognition of the respective species.

44. **Salix ligulifolia** Ball ex Schneider, Jour. Arnold Arb. **2:** 186, 188. 1922. TYPE: Syntypes from New Mexico, Colorado, Utah, Wyoming, and Nevada.

Salix lutea var. *ligulifolia* Ball, Bot. Gaz. **71:** 428. 1921. TYPE: above Ft. Apache, Arizona, *Coville 1977* (US).

Shrub to 5 m high; leaf blades narrowly elliptic or lanceolate, 1–10 cm long, entire or sometimes toothed, pale or glaucous beneath, glabrous or nearly so; stamens 2; anthers 0.4–0.8 mm long; pistillate aments appearing before or with the leaves, 1.5–6 cm long, sessile or with leafy floriferous branchlets to 10 mm long; capsules glabrous; stipes 1–2 mm long; styles 0.1–0.7 mm long; bracts brownish or black, pubescent, persistent. $2n = 38$.

Stream banks in the plains and foothills of Nevada, Arizona, New Mexico, southern Utah, Colorado, and southeast Wyoming. Additional distribution: California and southern Oregon.

See discussion under *S. lutea*.

45. **Salix monochroma** Ball, Bot. Gaz. **71:** 431. 1921. TYPE: valley of Hatwai Creek, Nez Perces Co., Idaho, *Sandberg, MacDougal, & Heller 39* (Lectotype here designated, pistillate specimen, US!).

Shrub to 4 m high; leaf blades ovate or lanceolate to elliptic-obovate, 2–10 cm long, shallowly toothed, not glaucous, glabrous except when young; stamens 2; pistillate aments appearing with the leaves, 2–6 cm long, with usually leafy floriferous branchlets 3–8(13) mm long; capsules glabrous; stipes (1.5)2–4 mm long; styles 0.2–0.7(1) mm long; bracts brown or black, usually pubescent, persistent.

Wet meadows and stream banks in Idaho and possibly northwest Wyoming and western Montana. Additional distribution: Washington, Oregon, and British Columbia.

See discussion under *S. lutea*.

XII. Section *Sitchenses* (Bebb) Schneider, Jour. Arnold Arb. **1:** 91. 1919. TYPE SPECIES: *S. sitchensis* Sanson ex Bong.

46. **Salix sitchensis** Sanson ex Bong., Mem. Acad. St. Petersb. VI, **2:** 162. 1832. TYPE: Sitka, Alaska, *Mertens* in 1827.

Shrub or tree-like, to 6 m high; leaf blades obovate, oblanceolate, or sometimes elliptic, 2–9 cm long, obtuse or rounded at tip, mostly entire, silvery-hairy beneath; stamens solitary; anthers 0.6–0.8 mm long; pistillate aments appearing before or with the leaves, 2–8 cm long, with leafy floriferous branchlets 5–20 mm long; capsules pubescent; stipes 1 mm or less long; styles 0.3–1 mm long; bracts black or brown, pubescent, persistent. $2n = 38$.

Stream banks in northwest Montana, northern Idaho, and western Nevada. Additional distribution: southern Alaska, British Columbia, Washington, Oregon, and California.

This species is often confused with *Salix scouleriana* but the silvery pubescence of the lower leaf surface and the solitary stamens are distinctive.

XIII. Section *Lanatae* Koehne, Deutsche Dendrol. 87. 1893. TYPE SPECIES: *S. lanata* L.

47. **Salix barrattiana** Hook., Fl. Bor. Am. **2:** 146. 1838. TYPE: Rocky Mountains of Canada, *Drummond* (Holotype, K; fragment A!).

Shrub to 1.5 m high; leaf blades elliptic or sometimes oblanceolate, 2–7 cm long, usually pubescent and entire or minutely serrulate; stamens 2; anthers 0.5–0.8 mm long; pistillate aments appearing before or with the leaves, some usually terminating growth of previous season, 4–9 cm long, usually sessile or nearly so; capsules pubescent; stipes less than 1 mm long; styles 1–2.5 mm long; bracts brown or black, pubescent, persistent.

Alpine and subalpine on the Beartooth Plateau of Montana and Wyoming and in Glacier Park, Montana. Additional distribution: Alaska, Yukon, District of Mackenzie, Alberta, and British Columbia.

The glutinous twigs are very distinctive and stain pressing papers yellow or green.

48. **Salix tweedyi** (Bebb ex Rose) Ball, Bot. Gaz. **40:** 377. 1905.

Salix barrattiana tweedyi Bebb ex Rose, Contr. U. S. Natl. Herb. **3:** 572. 1896. TYPE: Big Horn Mountains, Wyoming, *Tweedy 11* (Lectotype by Ball 1905, US!).

Salix rotundifolia Nutt., N. Am. Sylva **1:** 75. 1842, not Trautv. in 1832. TYPE: Thornburgh's Ravine, Idaho, *Nuttall s. n.* (Isotype, GH!).

Shrub to 4 m high; leaf blades elliptic, ovate, or obovate, 2–10 cm long, finely toothed, often slightly paler beneath, glabrous, or pubescent especially when young; stamens 2; anthers 0.5–0.9 mm long; pistillate aments appearing before or with the leaves, some at tips of twigs of previous year, 3–9 cm long, sessile or with floriferous branchlets to 10 mm long; capsules glabrous; stipes 0.2–1.2 mm long; styles 1–3 mm long; bracts dark brown or black, pubescent, persistent.

Stream banks and wet meadows in the mountains of Wyoming, Montana, and Idaho. Additional distribution: north-central Washington.

This species normally has very long and stout aments, some of which appear terminal on twigs of the previous year. The branchlets often have long, spreading hairs. The species seems to be common only in a few areas such as the Teton Range, Wyoming; the Beartooth Plateau area of Montana and Wyoming; and southern Gallatin and Park Counties, Montana.

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BOX 1471

RAWLINS, WYOMING 82301

NOTES ON MIDDLE AMERICAN BIGNONIACEAE

ALWYN H. GENTRY[1]

Recent collections of Bignoniaceae include three new species of *Amphitecna* from Guatemala and Chiapas. In addition the two new combinations needed for the checklist of Belize plants being published in this journal (Spellman, Dwyer & Davidse, 1975; Dwyer & Spellman, in preparation) are proposed. One of these derives from a proposed generic merger — *Neomacfadya* with *Arrabidaea*. Several Belize taxa should be known by names other than those used in the *Flora of Guatemala* (Standley & L. Williams, 1974); these changes are briefly noted below with the names used in the *Flora* in parentheses. For complete synonymies see the cited reference or my *Flora of Panama* treatment (Gentry, 1973b).

NEW SPECIES OF AMPHITECNA

Most genera of Bignoniaceae have wind-dispersed seeds and wide-ranging species which often extend from Mexico to Argentina. Local endemics are exceedingly rare in such genera with the second collection of new species described, for example, from Amazonian Brazil as likely to turn up in Venezuela or Peru as Brazil (Gentry, 1974; Sandwith, 1939). Thus all but seven of the 57 wind (or water) dispersed species of Bignoniaceae native to northern Central America reach northern South America. In dramatic contrast the indehiscent-fruited species of *Amphitecna* and *Parmentiera* with mammal-dispersed seeds have very localized distributions. None of the 13 primarily mammal-dispersed species of Bignoniaceae native to northern Central America is known to occur outside the region. Similarly none of the eight mammal-dispersed species of Panama and Costa Rica occurs elsewhere as compared to the 78% of wind or water dispersed species which reach northern Central America and the 88% which reach Venezuela (Gentry, 1974). Several species of Crescentieae are apparently endemic to single mountains or even specific rock outcrops (Gentry, 1974, 1976c). In light of these generalizations, the discovery of several new species of *Amphitecna* in northern Central America may be seen in perspective as a reflection of predictable evolutionary tendencies rather than an exercise in taxonomic splitting.

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Amphitecna costata A. Gentry, sp. nov. Figure 1A

Arbor parva. Folia alterna, obovata vel obovato-elliptica, acuminata, venulis albo-marginatis. Inflorescentia uniflora, flore in brachyblasto bracteato in trunco; calyx bilabiatus; corolla pallide viridis, campanulata, lobis connatis; stamina subexserta; ovarium oblongum, longitudinaliter striatum. Fructus indehiscens, cylindricus, longitudinaliter costatus.

Small tree 3–14 m. tall; branchlets angulate, the surface smooth, tannish. Leaves simple, alternate, usually clustered near tips of twigs, obovate to obovate-elliptic, sharply acuminate (the acumen 1–3 cm. long), cuneate at base, 21–50 cm. long, 6.5–18 cm. wide, coriaceous, glabrous throughout, midrib raised slightly above and conspicuously below, secondary veins 10–16 on a side, plane above, prominulous below, tertiary venation perfectly plane and conspicuously whitish-margined below (cf. *A. silvicola* L. Wms.), drying gray or olive gray with the main veins darker below, petiole poorly differentiated, occasionally to 1 cm. long but winged at top and merging with leaf base. Flowers cauliflorous, mostly near base of trunk, mostly borne singly at the nodes from fascicles of small bracts, the pedicels 2–2.5 cm. long, the calyx bilabiate, 1.3–1.5 cm. long, the lobes obtuse to subapiculate, glabrous; corolla pale green with the lobes pale lilac-pinkish, tubular-campanulate, ca. 3.5 cm. long, the lobes completely fused; stamens subexserted, the anther thecae divergent, 4–5 mm. long; pistil ca. 3.5 cm. long, the ovary oblong, 3–4 mm. long, prominently longitudinally striate; disc annular-pulvinate, ca. 6 mm. wide. Fruit cylindrical, tapered to both ends, prominently longitudinally costate, 22–36 cm. long, 6–7 cm. wide, the seeds embedded in the whitish pulp.

TYPE: **Guatemala.** IZABAL: Rio Juyama, southeast of Cheyenne, 15 miles southwest of Bananera, 50–100 m., 8 Apr 1940, *Steyermark 39130* (Holotype, F 1042987; isotypes, F 1042929, 1055459).

Endemic to low altitudes in Izabal Department, Guatemala.

ADDITIONAL COLLECTION EXAMINED: **Guatemala.** IZABAL: along Rio Tameja, alt. 50 m., shrub 10–15 ft. tall, *Steyermark 41796* (F, US).

This species was confounded with *Amphitecna macrophylla* (Seem.) Miers ex Baill. in the *Flora of Guatemala* and the fruit and flowering branch (but not the leaf nor corolla) illustrated for that species are actually *A. costata.* The very different leaves of

A. macrophylla are much larger ((40–)50–100 cm. long, to 35 cm. wide) and oblanceolate while its fruit (Figure 1H) is shorter and angulate rather than long, cylindrical, and costate as in *A. costata*. These two species are ecologically and altitudinally separated. *Amphitecna macrophylla* occurs farther west in Guatemala in Alta Verapaz and Huehuetenango Departments and only at higher altitudes between 300 and 1500 m. It is reported to be locally very common on limestone, especially around 1000 m. I have also seen sterile collections of *A. macrophylla* from the states of Oaxaca and Veracruz in Mexico.

Amphitecna breedlovei A. Gentry, sp. nov. Figure 1C, D.

Arbor parva. Folia alterna, obovata vel oblanceolata, coriacea, sessilia, infra venis secundariis prominentibus. Inflorescentia uniflora, flore terminali; calyx profunde bilabiatus; corolla albida, campanulata, lobis connatis; ovarium ovoideum. Fructus indehiscens, oblongo-ellipsoideus, apiculatus, laevis.

Small tree 7–8 m. tall; branchlets conspicuously angulate when young, subterete when older. Leaves simple, alternate, obovate to oblanceolate, acute to rounded at apex (often more or less apiculate), more or less cuneate at base, 5–18 cm. long, 1.7–6 cm. wide, coriaceous, glabrous throughout except for scattered lepidote scales, midrib noticeably raised above and especially below, secondary veins 8–14 on a side, prominent below, plane and hardly visible above, the main veins below drying tannish against an olive-gray surface, petiole essentially absent. Flowers (description includes *Breedlove 32819*, see below) terminal, borne singly, the calyx 1.5–2 cm. long, bilabiately split to near base, pedicel 2.5–4.5 cm. long; corolla white, campanulate, 3–4 cm. long, 1.5–1.8 cm. wide at mouth of tube, the lobes completely fused; ovary 2 mm. long, 2 mm. wide, disc 2 mm. long, 7 mm. wide. Fruit a pepo or calabash,

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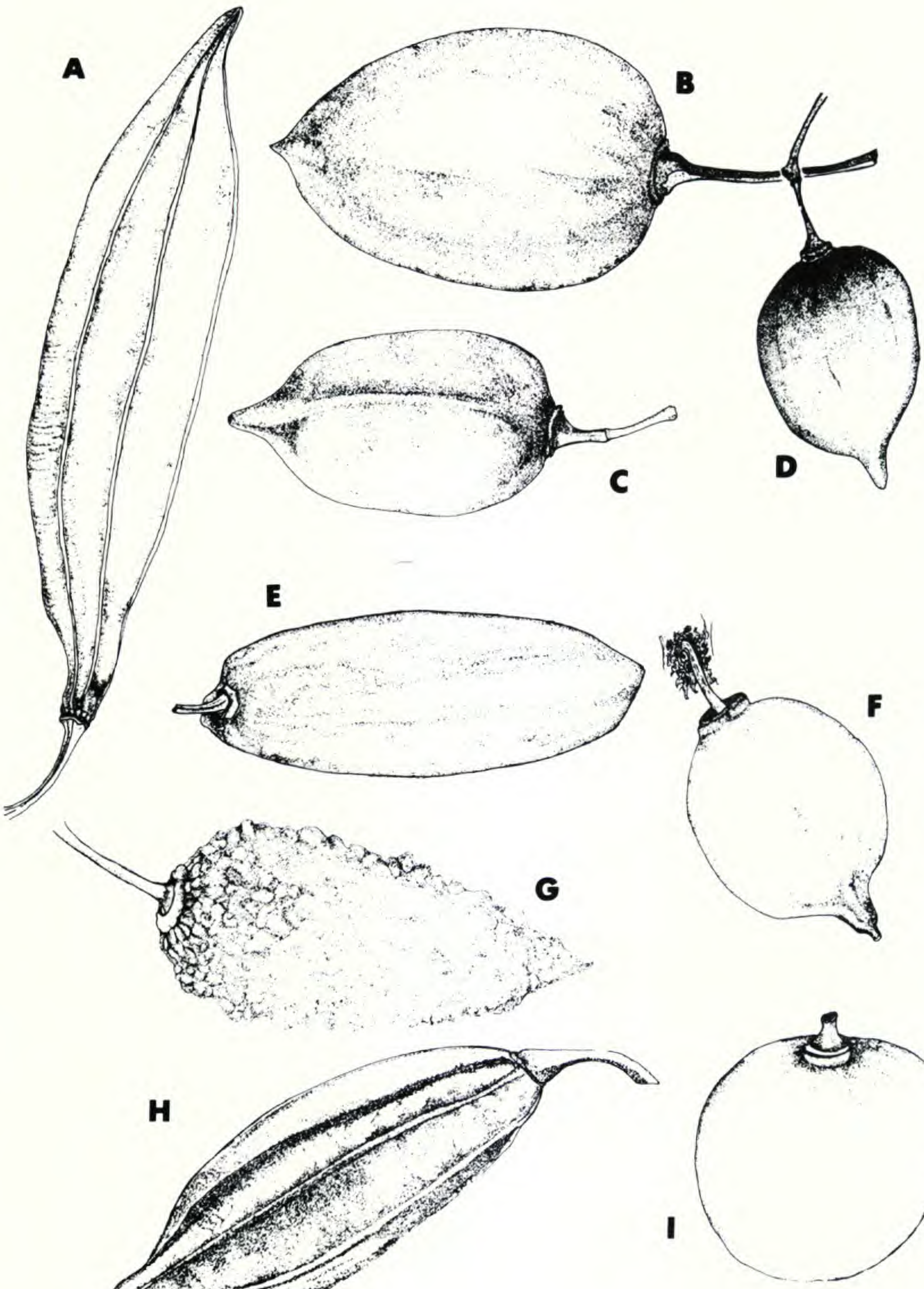
Figure 1. Fruits of some Middle American species of *Amphitecna*, all × 1/3. A, *A. costata* A. Gentry (after *Steyermark 39130*); B. *A. montana* L. Wms. (after *Breedlove 22260*); C, *A. breedlovei* A. Gentry (after *Breedlove 24946*); D, *A. breedlovei* A. Gentry (after *Breedlove 38684*); E, *A. silvicola* L. Wms. (after *Breedlove 38800*); F, *A. apiculata* A. Gentry (after *Breedlove 33928*); G, *A.* cf. *steyermarkii* (A. Gentry) A. Gentry (after *Breedlove & McClintock 34091*); H, *A. macrophylla* (Seem.) Miers ex Baill. (after Griggs, 1904); I, *A. latifolia* (Mill.) A. Gentry (after *Liesner 1384*).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oblong-ellipsoid, apiculate, smooth-surfaced, 10 cm. long (including the 1.5 cm. long apiculation), about 5 cm. in diameter.

TYPE: **Mexico.** CHIAPAS: Municipio Villa Corzo, 10–12 km. SW of Colonia Agronomos Mexicanos along a logging road to the ridges of Cerro Tres Picos, slopes with *Pinus* and *Quercus* along a stream with *Ficus* spp., 1000 m. alt., 4 May 1972, *Breedlove 24946* (Holotype, CAS).

Slopes of Rio Grijalva Valley in western Chiapas from 850–1000 m. in the Municipios of Villa Corzo and Ocozocoautla, montane rain forest and evergreen seasonal forest habitats (sensu Breedlove, 1973).

ADDITIONAL COLLECTIONS EXAMINED: CHIAPAS: Municipio Villa Corzo, 65 km. S of Mexican Highway 190 on road from Tuxtla Guttierrez to Nuevo Concordia, steep canyon with seasonal evergreen forest and slopes of *Quercus*, 850 m. alt., *Breedlove 37732* (CAS). Municipio Ocozocoautla, Rancho Concepcion y Cerro Brujo, *Miranda 5154* (US).

A similar plant but with leaves tapering to a long narrow tip and a shorter fruit (Figure 1D) which is almost globose except for the acumen occurs at lower altitudes between 550 and 700 m., also on the slopes bordering the Rio Grijalva. This is presumably a variant of *Amphitecna breedlovei* and is represented by two collections:

Municipio Ocozocoautla: Forest just above community and lake of Malpaso, 45 km. N of Ocozocoautla, 550 m. alt., steep ravines with "lower montane rain forest", *Breedlove 32819* (CAS); 46 km. N of Ocozocoautla on road to Mal Paso, "lower montane rain forest", 700 m., *Breedlove 38684* (CAS).

Amphitecna breedlovei differs very little in vegetative or floral characters from *A. donnell-smithii* (Sprague) L. Wms. with a similar but more eastern range in Izabal, Alta Verapaz, and extreme southern Petén Departments of Guatemala at altitudes from 50 to 350 m. (*Beaman 5206* (MO) from 450 m. in the Serrania de Los Tuxtlas, Veracruz State is probably also *A. donnell-smithii* indicating that it occurs in Tabasco and extreme northern Chiapas as well). The major difference between *A. donnell-smithii* and *A. breedlovei* is the former's much longer more cylindrical fruit — similar to *A. montana* L. Wms. (Figure 1B) but narrower, or to *A. silvicola* (Figure 1E) but tapering to an acute or subacuminate point. Most specimens of *A. donnell-smithii* have thinner more membranaceous leaves with distinct slender petioles sometimes to 1 cm. long. The leaves of *A. donnell-smithii* are always acuminate

(the tip usually 1–2 cm. long) and narrowly tapering to the base which differentiates them from typical *A. breedlovei* but not from the lower Grijalva valley form.

Amphitecna apiculata A. Gentry, sp. nov. Figure 1F

Arbor parva. Folia alterna, anguste obovata, acuta vel acuminata, subcoriacea vel chartacea, infra venis secundariis prominentibus. Inflorescentia pauciflora, floribus plerumque terminalibus; calyx leviter 2–3-labiatus; corolla albida, tubularis, lobis connatis, vix calycem excedens; ovarium ovoideum. Fructus indehiscens, apiculatus, cetero globosus vel ellipsoideus, laevis.

Small tree 4–13 m. tall; branchlets conspicuously angulate when young, subterete when older. Leaves simple, alternate, narrowly obovate, acute to acuminate at apex, more or less cuneate at base, (10–)15–35 cm. long, (3–)5–10 cm. wide, (some leaves of every collection at least 20 by 6 cm.), subcoriaceous to chartaceous, glabrous throughout except for a very few minute scattered lepidote scales, midrib raised slightly above and prominently below, secondary veins 10–15 on each side, prominulous above and prominent below, the main veins usually drying tannish against a grayish-olive surface, petiole essentially absent. Flowers mostly terminal, sometimes in part ramiflorous from bracteate short-shoots, borne singly or in fascicles of 2 or 3, the pedicels 3.5–5 cm. long; calyx campanulate, 16–20 mm. long, 9–10 mm. wide, glabrous, irregularly 2–3-labiately split in upper third or half; corolla white, more or less tubular, barely exceeding calyx, 2.2–2.8 cm. long, ca. 1 cm. wide at top of tube, the lobes more or less fused into an inconspicuous rim, lobes stalked-lepidote outside, tube glabrous outside, glabrous inside except a few stalked-lepidote glands near level of stamen insertion; stamens inserted ca. 10 mm. from base of tube, the filaments 1–1.3 cm. long, the thecae thick, hardly divergent, 3 mm. long; ovary ovoid, 2 mm. long, 1.5 mm. wide, densely lepidote; unilocular except at base with the ovules on two parietal placentae; disc ca. 1 mm. long and 3 mm. wide.

TYPE: **Mexico.** TABASCO: San Isidro, Balancan, 7–11 Jun 1939, *Matuda 3388* (Holotype, MO 1172883; isotype, MO 1198258).

Occurring in the moist lowlands along the Rio Usumacinta in extreme northeastern Chiapas and adjacent Tabasco from 50(?)–350 m. altitude. A single fruiting collection from central Veracruz State also appears to be conspecific.

ADDITIONAL COLLECTIONS EXAMINED: **Mexico.** CHIAPAS: Municipio Palenque, 6–12 km. S of Palenque on road to Ocosingo, slopes and small streams with "tropical rain forest" along the ridges, 300 m., tree 40 ft., flowers white, *Breedlove 28886* (CAS). Municipio Ocosingo, limestone ridges, tropical rain forest at the ruins of Yaxchilan, banks of Rio Usumacinta, 300 m., tree 40 ft. tall, *Breedlove 33928* (CAS). Municipio Ocosingo, tropical rain forest along small streams near the settlement of Lacanja, 350 m., tree 40 ft. tall, *Breedlove 34472* (CAS). VERACRUZ: Municipio Nautla, La Martinica, bosque de *Ficus*, terreno plano, 50 m., arbusto de 4 m. de alto, fruto verde, escaso, *Ventura 3341* (F).

Amphitecna apiculata matches only *A. breedlovei* in having conspicuously apiculate fruits (Figure 1F). It differs from *A. breedlovei* in the larger (for the most part much larger) leaves, very different calyx and corolla, and lowland habitat. *Amphitecna apiculata* differs from lowland *A. donnell-smithii* in the apiculate fruit, much larger leaves, the much narrower corolla, and the calyx not split to near base.

Amphitecna steyermarkii (A. Gentry) A. Gentry, Taxon **25:** 108. 1976.

This species is remarkable in the genus in its spathaceously split calyx, a feature shared only with Panamanian *Amphitecna spathicalyx* (A. Gentry) A. Gentry. It was described from Guatemalan material lacking fruits. To the two collections previously known may be added a recent gathering from just across the Mexican border in Chiapas — *Breedlove 39067* (CAS) from 1000 m. near Frontera Comalpa. Several additional collections are perhaps forms of *A. steyermarkii.* These include the following:

Mexico. CHIAPAS: Municipio Solosuchiapa, 2–4 km. below Ixhuatan along road to Pichucalco, 1200 m., *Breedlove 34896* (CAS). Municipio Las Margaritas, confluence of Rio Ixcan with Rio Lacantum on Guatemala border, 300 m., *Breedlove & McClintock 34091* (CAS). VERACRUZ: Municipio Santiago Tuxtla, summit of Cerro Vigia, 950 m., *Beaman 6404* (MO).

None of the material cited above is at anthesis so it is impossible to verify whether the calyx is spathaceous or not. Vegetatively these large-leaved collections are closer to *Amphitecna steyermarkii* than to any other species; if not conspecific, they represent yet another undescribed taxon. Two of these specimens are of fruiting material and the fruit (Figure 1G) is most distinctive. The fruit is ellipsoid to narrowly ovoid, tapering to an acute but non-apiculate apex, strikingly rough-surfaced, 11–13 cm. long and 5–6 cm. in diameter. It is possible that the unusual surface texture is a result of abnormal growth but even in shape these fruits are unlike those

of any other species of northern Central America. Additional material of this complex is urgently needed.

Amphitecna montana L. Wms., Fieldiana, Bot. **36:** 22. 1973.

This species was based on material from the Volcan Tajumulco region in extreme southwestern Guatemala (San Marcos Department) and adjacent Chiapas. Its lowest recorded altitude is 1900 m. It is well characterized by distinctly petiolate leaves, long pedicel, and circumscissile bilabiate calyx. The fruit (Figure 1B) is wider than in other *Amphitecna* species from northern Central America and borne on a longer pedicel.

Two rather fragmentary collections from outside this geographical area may tentatively be referred to *Amphitecna montana* on the basis of their long petiolate leaves. *Steyermark 48766* (F) from 17 miles north of Barillas, Sierra de los Cuchumatanes, has more coriaceous leaves than any other collection of *A. montana* and comes from a lower altitude (1500 m.) than any of the Tajumulco area collections. The fruits, apparently not preserved, are described by the collector as 6 inches long and 3 inches in greatest diameter, dimensions that fit those for *A. montana.* A second problematical collection with long petiolate leaves comes from Montana de Celaque in Lempira Department, Honduras. The Honduran collection, *Hazlett 2287* (MO), includes a single detached flower with a gigantic (3.5 by 3.1 cm.), apparently spathaceously split calyx, a short corolla only 3.5 cm. long, and conspicuously exserted anthers. Either or both of these may prove specifically distinct from *A. montana.*

Amphitecna silvicola L. Wms., Fieldiana, Bot. **36:** 25. 1973.

This montane species was known only from the type collection from Chiapas when described; its fruit was unknown. Thanks to the recent effort of Dennis Breedlove and associates, *Amphitecna silvicola* is now known from four additional collections all from 1300–1400 m. near the type locality in the Municipio of La Trinitaria, Chiapas. Its fruit (Figure 1E) proves to be narrowly oblong-ellipsoid, obtuse to acute or short-acuminate, 14–15 cm. long, 4–5.5 cm. wide, the surface smooth and black-drying, the seeds ca. 1.3 cm. long and 1.5 cm. wide, embedded in the pulp. Several collections from 800–1200 m. altitude in Alta Verapaz, Guatemala, are probably also *A. silvicola* although not referred to this species in the *Flora of Guatemala.* These collections, which include only a single

fertile sheet with two flowers, have longer leaves than the Chiapas material and more prominulous secondary veins and less conspicuously white-edged venation beneath. They include *Standley 70325* (F, US) from the region of Cocola, northeast of Carcha, *Standley 70148* (F, US) from Saquija, 43 km. NE of Coban, and *Johnson 867* (US) from Quebradas Secas. Collections from the intermediate Cuchumatanes region are needed to resolve the taxonomic status of the Alta Verapaz plant.

Several more species of *Amphitecna* undoubtedly remain undescribed. *Matuda 17649* (F) from Corcega, Pueblo Nuevo, Chiapas, has a narrowly oblong almost square-based fruit quite unlike any of the known species. Several of the anomalous Veracruz collections discussed above may also prove specifically distinct when adequate material becomes available for analysis of patterns of variation.

NOTES ON BELIZE AND GUATEMALA SPECIES

1. **Adenocalymma inundatum** Mart. ex DC., Prodr. **9:** 201. 1845.
   A. calderonii (Standl.) Seib. — See Gentry, 1976a.

2. **Amphitecna latifolia** (Mill.) A. Gentry, Taxon **25:** 108. 1976.
   A. obovata (Benth.) L. Wms. — changes in the Code of Nomenclature adopted by the Leningrad Congress mandate choice of *Amphitecna* over *Dendrosicus* for this genus (Gentry, 1976b).

This combination needs additional justification in light of Williams' (1975) contention that Miller's *Crescentia latifolia* and all names for which it serves as basionym should be rejected as ambiguous. As I have previously noted (Gentry, 1973c), Miller (1768) treated two species of *Crescentia,* both of which are recognizable from their descriptions alone. His *C. latifolia, ex descriptione,* is the widespread species which until recently has been called *Enallagma latifolia* (Mill.) Small. In addition to a description Miller cited Plumier's (1703) *Cuiete latifolia, fructu putamine fragili* as a synonym, even deriving his specific epithet "latifolia" from Plumier. Plumier's (1703) generic illustration of *Cuiete* shows flowers, fruits and seeds all unmistakably belonging to this species. Later, in his *Plantarum Americanarum,* Plumier (1757) repeated the *same* illustrations of flowers, fruits and seeds adding to them a vegetative branch with the characteristic broad leaves of this species. Williams

(1975) argues that *Crescentia latifolia* and names based on it should be rejected as ambiguous until "typified by something which Miller saw." In the apparent absence of voucher material prepared from the plants cultivated by Miller, I have proposed the 1757 Plumier plate (*pl. 109*) as a type illustration, while Williams rejects this on the hypothesis that Miller (1768), who cites only the earlier Plumier reference, may not have seen the Plumier plate. Since the 1757 Plumier plate *duplicates* the 1703 rendition, except for addition of a vegetative branch, whether Miller actually saw both plates or only the cited one is largely irrelevant. I consider the latter, which was available long before 1768, a better type illustration because of its inclusion of the wide leaves on which Miller's specific epithet is based. The differences noted by Williams between the leaf dimensions of Miller's description and the Plumier plate are taxonomically unimportant, reflecting merely the juvenile condition of the living plants available to Miller. Twenty-three juvenile leaves of a plant grown by me from seed of a large-leaved tree matching Plumier's illustration averaged 4.4 inches (10.4 cm.) long and 1.3 inches (3.1 cm.) wide as compared with Miller's "three inches in length and one and a quarter broad in the middle" and the smallest juvenile leaves measured only 5 by 1.5 cm. While it is regrettable that no Miller collection is available to serve as a type, there is no ambiguity as to identification of either Plumier illustration or Miller's description itself; rejection of Miller's epithet is unjustified.

3. **Arrabidaea costaricensis** (Kränzl.) A. Gentry, Brittonia **25:** 231. 1973.

A. litoralis (HBK.) Standl. sensu Flora of Guatemala.

4. **Arrabidaea podopogon** (DC.) A. Gentry, comb. nov.

Spathodea podopogon DC., Prodr. **9:** 205. 1845. TYPE: Cuba, *Sagra 293* (G-DC).
Macfadyena podopogon (DC.) Griseb., Cat. Pl. Cuba 195. 1866.
Neomacfadya podopogon (DC.) Baill., Hist. Pl. **10:** 26. 1888.
Neomacfadyena podopogon (DC.) Baill. ex K. Schum. in Engl. & Prantl, Nat. Pflanzenf. **4**(3b): 227. 1894.
Phryganocydia brevicalyx Standl., Field Mus. Bot. **4:** 261. 1929. TYPE: Belize (British Honduras), Tower Hill, *Karling 39* (Holotype, F; isotype, US).

Monotypic *Neomacfadya* was described from Cuba but its center of distribution is the Yucatan Peninsula where it occurs in Belize, Guatemala (Peten) and adjacent Mexico (Quintana Roo and Yucatan). Although reported as "exceedingly rare" in the *Flora of*

Guatemala, it is abundant in secondary forest associations throughout Belize and is one of the commonest species of Bignoniaceae in the country. The outstanding feature of *Neomacfadya* is a (reputedly) spathaceous calyx, the definitive characteristic of the genus. Its spathaceous (actually subspathaceous to bilabiate) calyx has led to comparisons with *Macfadyena* (Grisebach, 1866) and *Phryganocydia* (Standley, 1929) but its much closer relationship with *Arrabidaea* has been overlooked. Every characteristic of *Neomacfadya* is shared with *Arrabidaea* (sensu Sandwith, 1968): simple tendrils, leaves simple in part, interpetiolar glandular fields, corolla pale magenta with white throat and puberulous outside, linear fruit, thin bialate seeds. Even *Neomacfadya's* thin subspathaceous to bilabiate calyx and few-flowered axillary inflorescences are not out of place in *Arrabidaea* (including *Scobinaria,* see Gentry, 1977). *Neomacfadya* is, in fact, intermediate between *Arrabidaea* (which it resembles in most characteristics) and *Scobinaria* which it resembles in calyx and inflorescence. Inclusion of *Scobinaria* in *Arrabidaea* mandates a similar reduction of *Neomacfadya* with the single new combination proposed above.

5. **Arrabidaea pubescens** (L.) A. Gentry, Brittonia **25:** 239. 1973.

A. sieberi DC. — I recently found the missing Houstoun type material of *Bignonia pubescens* L. (based on Miller's (1759) *Bignonia bifolia frutescens, foliis subtus villosis, siliquis longissimus compressis*) filed with undetermined South American Bignoniaceae in the British Museum herbarium. The type represents the plant formerly known as *A. sieberi* as I had surmised from the description (Gentry, 1973a) and proves the identity of that species with *A. pubescens.*

6. **Arrabidaea verrucosa** (Standl.). A. Gentry, Selbyana **2:** 43. 1977.

Scobinaria japurensis (DC.) Sandw. sensu Flora of Guatemala.

7. **Ceratophytum tetragonolobum** (Jacq.) Sprague & Sandw.

C. tobagense (Urb.) Sprague & Sandw.

8. **Cydista aequinoctialis** var. **hirtella** (Benth.) A. Gentry, Brittonia **25:** 231. 1973.

C. sarmentosa (Bertol.) Miers.

9. **Distictis buccinatoria** (DC.) A. Gentry, Brittonia **25:** 237. 1973.

Pithecoctenium buccinatorium DC.

10. **Jacaranda copaia** ssp. **spectabilis** (Mart. ex DC.) A. Gentry, comb. et stat, nov.

J. spectabilis Mart. ex DC., Prodr. **9:** 229. 1845. TYPE: Brazil, Amazonas, *Martius s.n.* of 1819 (M).

J. copaia var. *spectabilis* (Mart. ex DC.) Bur. ex Bur. & K. Schum. in Mart., Fl. Bras. **8**(2): 287. 1897.

J. superba Pittier, Bol. Soc. Venez. Ci. Nat. **6:** 19. 1940. TYPE: Venezuela, Bolivar, *Williams 11537* (F, US).

The common widespread *Jacaranda* of Central America, northwest South America and Amazonia differs significantly from the related plant of lowland Guayana in a number of morphological characteristics. Vegetatively it has more numerous pinnae and leaflets per pinna and smaller acute (not obtuse) membranaceous to chartaceous (not subcoriaceous) rhombic-elliptic (not elliptic to oblong-elliptic), sessile or subsessile (not distinctly petiolulate) leaflets. The widespread *Jacaranda* has thinly woody capsule valves 3.3–6 cm. wide while the Guayana area plant has thick woody capsule valves 7–10 cm. wide. I can detect no floral differences. The type of *J. copaia* (*Aublet s.n.* (P-AD 12304)) comes from the Guayana population; the widespread form has been described as *J. spectabilis* and as *J. superba.*

These two plants have generally been treated as constituting a single species following Bureau & K. Schumann's (1896–97) *Flora Brasiliensis* treatment. The acute-leafleted widespread form was reduced to varietal status by Bureau & K. Schumann on the basis of five mostly fragmentary collections — three of the Guayana plant and two (one from Panama and one from Amazonian Brazil) of the widespread form. The patterns of variation between the two populations were hardly evident from the scanty herbarium material then available, and distinction at the varietal level seemed appropriate.

The abundant additional material now available shows not only that the differences between these two entities are constant but also that they have mutually exclusive ranges (Figure 2). At least in Venezuela the range difference is ecologically correlated. The plant with round-tipped oblong-elliptic leaflets occurs only in the swampy lowland forest of Delta Amacuro (and adjacent extreme eastern Monagas State) while the form with acute rhombic leaflets occurs in well drained tropical moist forest through most of western and

Figure 2. Distribution of *Jacaranda copaia* (Aubl.) D. Don ssp. *copaia* (stars) and *J. copaia* ssp. *spectabilis* (Mart. ex DC.) A. Gentry (circles).

southern Venezuela including parts of Bolivar and Monagas States immediately adjacent to the Delta Amacuro swamp forest.

Taxonomically, these differences warrant more than varietal recognition and are certainly greater than those between several currently recognized *Jacaranda* species. Nevertheless the two forms of *J. copaia* are very closely related and relatively isolated from other species of the genus. In consideration of the wide use of the epithet *copaia* throughout the ample range of the acute-leafleted entity, I opt for its subspecific recognition as *J. copaia* ssp. *spectabilis*.

11. **Lundia puberula** Pittier, Contr. U. S. Natl. Herb. **18:** 258. 15 Sept. 1917.

L. dicheilocalyx Blake, Contr. Gray Herb. **52:** 94. 28 Sept. 1917.

12. **Mansoa verrucifera** (Schlecht.) A. Gentry, Ann. Missouri Bot. Gard. **63:** 62. 1976.
Adenocalymma fissum Loes.

13. **Pachyptera hymenaea** (DC.) A. Gentry, Brittonia **25:** 236. 1973.
Pseudocalymma sagotii (Bur. & K. Schum.) Sandw. sensu Flora of Guatemala.

14. **Pachyptera standleyi** (Steyerm.) A. Gentry, Brittonia **25:** 236. 1973.
Pseudocalymma sagotii var. *macrocalyx* (Sandw.) L. Wms.

15. **Pithecoctenium crucigerum** (L.) A. Gentry, Taxon **24:** 123. 1975.
P. echinatum (Jacq.) "K. Schum."

16. **Pseudocatalpa caudiculata** (Standl.) A. Gentry, Brittonia **25:** 241. 1973.
Mussatia caudiculata (Standl.) Seib.

17. **Stizophyllum riparium** (HBK.) Sandw., Lilloa **3:** 462. 1938.
S. perforatum (Cham.) Miers sensu Flora of Guatemala.

18. **Tabebuia donnell-smithii** Rose, Bot. Gaz. **17:** 418, 5. 26. 1892.
Roseodendron donnell-smithii (Rose) Miranda — see Gentry 1976a.

19. **Tabebuia impetiginosa** (Mart. ex DC.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. **11:** 176. 1936.
T. palmeri Rose.

Two other species pairs are best treated as synonymous: *Amphitecna oblanceolata* L. Wms. with *A. donnell-smithii* (Sprague) L. Wms. and *Macfadyena mollis* (Sond.) Seem. (as used in Central America) with *M. uncata* (Andr.) Sprague & Sandw.

Four additional species which were not included in the *Flora* are now known from Guatemala — *Pleonotoma variabilis* (Jacq.) Miers (*Steyermark 39504,* Izabal Province, south-facing lower ridges of Cerro San Gil, opposite Cayuga, 30–500 m.) characterized by biternate leaves, square branchlets, and trifid tendrils and three of the *Amphitecna* species discussed above — *A. steyermarkii* (A. Gentry) A. Gentry, *A. silvicola* L. Wms., and *A. costata* A. Gentry.

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ALWYN H. GENTRY
MISSOURI BOTANICAL GARDEN
ST. LOUIS, MISSOURI 63110

OBSERVATIONS ON SOME UNCOMMON VASCULAR AQUATIC PLANTS IN NEW ENGLAND[1]

C. BARRE HELLQUIST

During the summers of 1971–1976 a number of uncommon taxa of vascular aquatic plants was discovered in New England. Pertinent information concerning these and their ranges are given here. Locations for the specimens referred to are listed at the end of the discussion of each taxon. Specimens have been deposited in the herbaria of Boston State College and various other institutions. Alkalinity data are in addition to that of Hellquist (1975).

Potamogeton filiformis Pers.

Potamogeton filiformis var. *borealis* (Raf.) St. John was found at numerous locations in Aroostook County, Maine, one location in Coos County, New Hampshire, and four locations in Caledonia County, Vermont. The only previously reported and verified Vermont specimens are from Otter Creek, Weybridge and Lake Champlain at North Hero and Charlotte. These collections are on deposit in the Pringle Herbarium of the University of Vermont.

Three of the four ponds in Caledonia County also contained the broader-leaved *Potamogeton filiformis* var. *macounii* Morong, and these collections are new records for New England. A specimen reported (Hellquist, 1972) from Lombard Pond, Colebrook, New Hampshire, as var. *borealis,* and a specimen of *P. filiformis* var. *borealis* collected by G. D. Chamberlain (*2278*) from Butterfield Lake, Caswell, Aroostook County, Maine, may both be var. *macounii.*

The Vermont plants are from shallow water (60.0 cm.). The lower leaves are slightly broader than the upper leaves, and the stipules of the lower leaves on some plants are inflated up to 2.9 mm. in width, as is *P. vaginatus* Turcz., but they are shorter in length (maximum 7.4 mm.). Stipules higher on the stem are longer (maximum 14.0 mm.). Fruits from the broader-leaved plants are identical with those of var. *borealis.*

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COLLECTION LOCATIONS: *Potamogeton filiformis* var. *borealis*.

Maine: AROOSTOOK CO.: Butterfield Lake, Caswell, *7779;* Pierce Lake, Caswell, *4470;* pond immediately east of Pierce Lake, Caswell, *4586;* Page Pond, Fort Fairfield, *7734;* Caribou Lake, Washburn, *4666*. **New Hampshire:** COOS CO.: Lombard Pond, Colebrook, *6219*. **Vermont:** CALEDONIA CO.: Harvey Lake, Barnet, *8726;* Warden Pond, Barnet, *4369, 9795;* Ewell Pond, Peacham, *8434, 9787;* Keiser Pond, Peacham, *8436, 9774*.

Potamogeton filiformis var. *macounii*. **Vermont:** CALEDONIA CO.: Warden Pond, Barnet, *6421, 9816;* Ewell Pond, Peacham, *8426, 9817;* Keiser Pond, Peacham, *8455, 9775*.

Potamogeton vaginatus Turcz.

Potamogeton vaginatus has been reported in eastern Canada, primarily from Newfoundland and Prince Edward Island (St. John, 1916). It was thought to be absent from New England, but it occurs to the west in the St. Lawrence River and the Finger Lakes region of New York. Muenscher (1944) indicates its presence in northern Maine, but I have seen no voucher specimen.

During the summer of 1973, I discovered an extensive population of plants that appear to be *Potamogeton vaginatus* growing at a depth of 1.5 meters in Prestile Stream, north of the dam at Mars Hill, Aroostook County, Maine. The leaves are broad (lower leaves 1.5 mm. and the upper leaves 0.6 mm. wide) and blunt-tipped. Stipule length is up to 4.5 cm. and twice as great as stem width. The spikes consist of seven to nine whorls of flowers. No fruits were found; this species rarely produces fruits.

This site was revisited during the summer of 1976. The population north of the dam was destroyed by lowering the water level for a period of time followed by flooding of the area. In the rapids south of the dam a few patches of *Potamogeton vaginatus* were observed. Here the plants were shorter in length — 25.0 cm. as compared to 1.0 m. north of the dam.

Alkalinity studies on this site, one in New York and 13 in Michigan indicate that *Potamogeton vaginatus* inhabits highly alkaline water. The results are recorded in Tables 1 and 2.

COLLECTION LOCATIONS: **Maine:** AROOSTOOK CO.: Prestile Stream pond north of the dam, Mars Hill, *7798;* Prestile Stream rapids south of the dam, Mars Hill, *11397*.

Potamogeton hillii Morong

Fernald (1932) considered *Potamogeton hillii* to be one of the

rarer species of *Potamogeton,* occurring in ten locations in five states. Since publication of Fernald's monograph, additional locations for this species have been reported, mainly from New England, New York, and Michigan. The most recent report from New England is that of Weber (1940) from Karner Brook, South Egremont, Massachusetts.

A survey of the previously reported New England collection sites has failed to reveal *Potamogeton hillii.* The population I discovered in 1972 at Cone Brook, Richmond, Massachusetts, was revisited in 1973 and the plant was found to be scarce. However, in 1974, I found it to be abundant. The area at South Stream, Pownal, Vermont, where the species was extremely abundant in 1973, was completely devoid of the plant in 1974. It appears that this species is sporadic and may be common only occasionally at certain locations. The other populations of *P. hillii* in Massachusetts are extensive and weedy.

My observations of *Potamogeton hillii* indicate that it is usually found in highly alkaline (Tables 1 & 2) shallow, muddy waters of ponds and streams. The populations at Tom Ball Brook, Alford, Massachusetts, are in water as deep as 1.5 meters, where its growth habit resembles that of deep-water *P. strictifolius.* In both shallow and deep water *P. hillii* was found fruiting freely.

During July 1976, an extensive population of flowering *Potamogeton hillii,* which contained some immature fruiting plants, was located in a marshy pond along Muddy Brook north of Stoney Brook Road, Great Barrington, Massachusetts. This population is of great interest as the leaves have three to seven veins instead of three as Haynes (1974) reports for the species. This makes recognition of this species and the hybrid *P.* × *longiligulatus* difficult as about one mile upstream there is a population of sterile five to seven veined plants, which appear to be *P.* × *longiligulatus.*

COLLECTION LOCATIONS: **Vermont:** BENNINGTON CO.: South Stream Pownal, *8140, 9670.* **Massachusetts:** BERKSHIRE CO.: small pond west of Tom Ball Brook, West Street, Alford, *9694;* marsh west of pond, west of Tom Ball Brook, Alford, *9697;* Muddy Brook at Blue Hill Road, Great Barrington, *9946;* marshy portion of Muddy Brook ca. 0.2 miles north of Stoney Brook Road, *9705;* Cone Brook, Richmond, *4489;* Fairfield Pond, Richmond, *11838;* pond east of junction of Rossiter Road and West Road, Richmond, *11837;* swamp along the south branch of Lily Brook at Bean Hill Road, Stockbridge, *9684.*

Table 1.

Tolerance of taxa to total alkalinity ($CaCO_3$) from New England waters.

Species	Mean	Median mg/l $CaCO_3$	Range	Number of Sites
Potamogeton hillii	141.9	116.0	86.0–290.0	10
Potamogeton × longiligulatus	96.0	90.0	71.5–130.0	4
Potamogeton vaginatus	103.5	103.5		
Najas guadalupensis	25.7	33.5	19.5– 41.5	5

Potamogeton X longiligulatus Fernald

This perplexing plant of alkaline waters (Tables 1 & 2) has received much attention by Voss (1972), Haynes (1974), and Haynes and Williams (1975). Fernald (1932) originally described *Potamogeton longiligulatus* from Newfoundland and indicated that no fruit was found. *Potamogeton longiligulatus* from Michigan is sterile and believed to be a hybrid between *P. strictifolius* and *P. zosteriformis* (Voss 1972, Haynes 1974). Studies by Haynes and Williams (1975) indicate this supposition to be the case. *Potamogeton longiligulatus* from East Creek, Orwell, Vermont, is apparently the hybrid between *P. strictifolius* and *P. zosteriformis,* as both species were present.

Ogden (1974) proposed the possibility of *Potamogeton hillii* as one of the parent species of *P. × longiligulatus* in eastern New York. This apparent hybrid was found in fruit by Smith and Ogden (*45590*), from Beebe Pond, Canaan, Columbia County, New York. During the summer of 1974, I visited this pond and a small number of fruits were collected. *Potamogeton zosteriformis* was abundant, and *P. hillii* was also found. *Potamogeton strictifolius,* however, was not found here.

I found *Potamogeton × longiligulatus* at Evarts' Pond, Windsor, Vermont, and at Mill Pond, South Egremont, Massachusetts. The parents of the two hybrid populations are not certain, as only one of the three possible parental species was found in each pond. *Potamogeton strictifolius* was common in Evarts' Pond, and *P. zosteriformis* was common at the Mill Pond. *Potamogeton hillii* was collected previously from both ponds and possibly may be one

Table 2.

Tolerance of taxa to total alkalinity ($CaCO_3$) from United States waters.

Species	Mean	Median mg/l $CaCO_3$	Range	Number of Sites
Potamogeton hillii	128.5	121.0	86.0–290.0	24
Potamogeton × *longiligulatus*	120.7	121.0	71.5–162.0	10
Potamogeton vaginatus	142.3	131.0	86.5–390.0	15
Najas guadalupensis	83.3	46.5	19.5–215.0	11

of the parents. During 1974 an extensive population of *P.* × *longiligulatus* was found among fruiting *P. hillii* at Muddy Brook, Great Barrington, Massachusetts. *Potamogeton zosteriformis* was not located although it appeared to be the other parent. The stipules of this hybrid were brown, slightly fibrous, and thus similar to those of *P. hillii.* The leaves are broad (2.9–3.6 mm.) with five to seven veins. Plants of this particular population appear to be similar to *P. hillii* and may be a backcross of the hybrid with *P. hillii.*

One of the supposed parents of some of the *Potamogeton* × *longiligulatus* hybrids from the eastern United States (*P. strictifolius*) rarely fruits, while *P. hillii* fruits abundantly. This may help to substantiate the parentage, particularly for the Beebe Pond, New York, population which was found in fruit.

Potamogeton × *longiligulatus* is known to be a hybrid of *P. strictifolius* and *P. zosteriformis* in Michigan. However, in New England and eastern New York more than one set of parents may give rise to a hybrid of the same description. None of the three proposed parents has been reported from Newfoundland where the type specimen was collected. In an unsuccessful attempt during 1976 to clarify the hybrid parentage of this taxon, ponds south of Flowers Cove, Newfoundland, were investigated for the holotype population. Perhaps the name *P.* × *longiligulatus* should not be utilized for all the different possible hybrids.

COLLECTION LOCATIONS: **Vermont:** ADDISON CO.: East Creek, Orwell, *8288.* WINDSOR CO.: Evarts' Pond (Lake Runnemede), *4462.* **Massachusetts:** BERKSHIRE CO.: Muddy Brook south of Blue Hill Road, Great Barrington, *9704, 9947.*

Potamogeton lateralis Morong

This species is one of the rarest pondweeds in the United States. Fernald (1932) noted only two locations from New England. These localities were the Charles River in Dedham and Needham, Massachusetts, and in Salisbury, Connecticut. I discovered *Potamogeton lateralis* in a small pond in Lancaster, New Hampshire, where it was extremely abundant, forming an extensive mat over most of the pond. The leaves were narrow (0.5–0.9 mm.) and acute-tipped. Sterile plants with floating leaves and fruiting plants without floating leaves were found. The fruits were similar to the isotype specimen in the Gray Herbarium. *Potamogeton lateralis* was not observed here in 1973, but in 1974 a few specimens were located. The sterile plants without floating leaves could easily be confused with *P. vaseyi.* This confusion would tend to support the statement of Ogden (1974), "Apparently closely related to *P. vaseyi,* it may be merely a variant of that species."

COLLECTION LOCATION: **New Hampshire:** COOS CO.: small unnamed pond along the north side of U. S. Route 2 ca. ¼ mile east of Vermont state line, Lancaster, *6387.*

Najas guadalupensis (Spreng.) Magnus

Najas guadalupensis, or southern naiad, is a common plant of the southern and central United States. Prior to 1926, this species was found at nine sites in New England. Five of these sites were in Massachusetts.

Four new locations, and the previously reported area of H. K. Svensen from Oyster Pond, Falmouth, Massachusetts, were located. Plants of *Najas guadalupensis* were found in waters of medium alkalinity (15.1–60.0 mg/l $CaCO_3$, Hellquist, 1975) as compared to the alkaline waters ($>$ 60.0 mg/l $CaCO_3$) outside of New England (Tables 1 & 2). Oyster Pond is brackish with a chloride reading of 1201.2 mg/l, indicating a tolerance of this species to higher salt content.

Najas guadalupensis was extremely common, forming weedy areas in Lake Waban, Massachusetts, Bantam Lake and Graniss Pond, Connecticut. Matthew Hickler, a student at the University of New Hampshire, discovered *N. guadalupensis* at Violin Pond, Wellesley, Massachusetts, during the summer of 1975. Upon visiting this pond during 1976 I did not find it. There were extensive stands of *N. flexilis* (Willd.) Rostk. & Schmidt present. Downstream from Vio-

lin Pond on the west side of Lake Waban *N. guadalupensis* was extremely abundant in approximately one meter of water. This population should be closely checked since Lake Waban drains into the Charles River, where it could become a problem as a water weed.

COLLECTION LOCATIONS: **Massachusetts:** NORFOLK CO.: Lake Waban, Wellesley, *11668;* Violin Pond, Rt. 135, Wellesley, *Matthew Hickler, 18 September 1975.* **Connecticut:** NEW HAVEN CO.: Graniss Pond, East Haven, *8596;* LITCHFIELD CO.: Bantam Lake, Morris, *8587.*

Najas minor All.

Discovered in the Hudson River, New York, in 1934 by Muenscher and Clausen, this European naiad has become very common in many locations along the Hudson River and west into Illinois (Meriläinen, 1968). The first record for this plant in New England was collected by William Countryman in Lake Champlain at Red Rock Bay, West Haven, Vermont, during 1965. It was misidentified as *Najas gracillima* (A. Br.) Magnus, with which it is often mistaken.

Najas minor was located for the first time in Massachusetts during the summer of 1974 at Lily Brook and Stockbridge Bowl, Stockbridge. At both locations the plant was extremely common and quite weedy. These sites were revisited in 1975, and *N. minor* was found only in Lily Brook. Directed at *Myriophyllum spicatum* L., a weed control program at Stockbridge Bowl has checked the spread of *N. minor*.

COLLECTION LOCATIONS: **Massachusetts:** BERKSHIRE CO.: Lily Brook east of Mahkeenac Rd. and Stockbridge Bowl, Stockbridge, *9688;* Stockbridge Bowl near inlet of Lily Brook, Stockbridge, *9687.*

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DEPARTMENT OF BIOLOGY
BOSTON STATE COLLEGE
625 HUNTINGTON AVENUE
BOSTON, MASSACHUSETTS 02115

QUERCUS × INTROGRESSA, A NEW HYBRID OAK

PAUL M. THOMSON

A previously undescribed hybrid which is believed to have involved three taxa in the genus *Quercus* L. is reported here from western Missouri. The taxa are: *Quercus muehlenbergii* Engelm., the chinquapin oak, *Q. prinoides* Willd., the dwarf chinquapin oak and *Q. bicolor* Willd., the swamp white oak. The hybrids are putatively the result of matings between introgressants of the two chinquapins (*Q. muehlenbergii* × *prinoides*) and *Q. bicolor.* While such matings in the published accounts of hybridization in *Quercus* have been suggested (Tucker, 1961, & Hardin, 1975), they have been infrequently noted and merit description. The name *Quercus* × *introgressa* was selected to emphasize the fact that one of the parental taxa is, in turn, of hybrid origin.

Quercus × introgressa Thomson, hybrida nova

Arbores 12–20 m altae trunco 47.7 ad 84.9 cm. diametro cortice cinereo fissili ramis patentibus. Ramuli hornotini laeves glabri vel pilis stellatis adspersis praediti. Gemmae apicales hiemales 3–5 ovatae usque rotundatae squamis ovatis 3–5. Folia obovata usque fere linearia, 6.7–15.5 cm. longi, 4.9–6.9 cm. lata, modice stellato-pilosa basi late vel anguste cuneata apice late acuta lobis 2–7 sinu 0.8–1.0 cm. profundo. Petioli 1.3–1.6 cm. longi. Glandes rotundatae vel ovoideae, 1.6–2.0 cm. longae, 1.2–1.6 cm. latae cupulis hemisphaericis pubescentibus squamis ovatis acutis pericarpio cupulam dimidio superante. Pedunculi 2.2–6.6 cm. longi, glabri.

TYPE: **United States:** MISSOURI: ca. 1 km. northeast of Concordia in a pasture adjacent to a rest area along Interstate 70, *P. Thomson 74–161* (Holotype, SIU; Isotype, MO).

Quercus × *introgressa* is known only from Lafayette County, Missouri, where there is a population of thirteen plants. Individuals of both parental taxa, three of *Q. muehlenbergii* × *prinoides,* and one of *Q. bicolor* are present on the site with the putative hybrids. The seventeen plants are situated in a cow pasture, midway on the northeast-facing slope of a low hill just above a small creek. I first observed them from an adjacent rest area along Interstate 70, approximately one kilometer northeast of Concordia, Missouri. It

would seem appropriate, therefore, that an individual of the taxon be colloquially referred to as a Concordia Oak.

Quercus × *introgressa* is most readily distinguished by its long peduncles which bear small, rounded fruit and by its short, narrow leaves. The hybrids are tree-sized plants ranging in height from 12–20 meters and in diameter (measured at breast height) from 47.7 to 84.9 centimeters. Although members of the population were found to be fertile, seedlings and saplings of both these and the parental taxa were not observed in the pastured area. However, the branches of one of the hybrids did extend from the fenced pasture into the rest area. Below these branches, in an area inaccessible to mowing, were several seedlings showing a resemblance to the hybrid tree. Collections were not made of the seedlings. The lack of smaller plants in the pasture is presumably due to what the owner described as heavy grazing by cattle and hogs on the site for many years (personal interview, 1974).

What is striking about the population is the presence of features among eight of the individuals that have values less than the same features in either typical *Quercus muehlenbergii* or *Q. bicolor.* It is believed that the source of this extreme variation in *Q.* × *introgressa* has been hybridization between *Q. muehlenbergii* introgressed by *Q. prinoides* and *Q. bicolor.* Figure 1 shows representative leaves from individuals of the taxa and the putative hybrids.

MATERIALS AND METHODS

Specimens of *Quercus muehlenbergii* Engelm. and *Q. prinoides* Willd. were selected and examined from populations occurring in western Missouri as well as in the herbaria of the Missouri Botanical Garden and Southern Illinois University at Carbondale. The putative hybrids are represented only from collections at the Concordia site and *Q. bicolor* only from herbarium material.

Data supporting hybridization are presented according to the methods of Anderson (1949) and involve only morphological features of the leaves and fruits. Characters used in this study include: lamina length, lamina width at the widest point, number of lobes, petiole length, peduncle length, nut length, nut diameter, and angle of the lamina base.

Three leafy twigs bearing acorns were removed from each field member. Leaf features were measured to the nearest millimeter

Figure 1. Leaf samples from *Quercus muehlenbergii* (lower left), *Q. prinoides* (lower right), an introgressant between them (lower center), *Q. bicolor* (top) and two hybrids (center).

for the terminal leaf of each twig and averaged to represent the individual. Number of lobes per leaf, excluding the terminal lobe, was determined by counting all those occurring between the base and the apex on the right side from the adaxial surface. Numbers were rounded off to the nearest lobe. Angle of the lamina base was determined by attaching a dissecting pin to a 15 centimeter plastic ruler at the zero mark and at right angles to it. Measurements were made by placing the tip of the pin at the junction of petiole and lamina and the shank along the margin of the base. The point at which the ruler crossed the midrib was recorded and divided by the length of the pin. The obtained value yielded the tangent of the angle formed by midrib and margin at the base. Because a ten centimeter pin was impractical for measuring smaller leaves, a five centimeter pin was used for the triangle's base and the value on the ruler was doubled to produce the tangent. Tangent values were converted to degrees from trigonometric tables. Values obtained for the three leaves were averaged and rounded off to the nearest degree. Fruit characters of the individuals were measured and averaged in a manner similar to that for leaf dimensions.

Measurements obtained from herbarium material do not represent averages for individuals, but a sufficient number of specimens was examined to gain an impression of the range of variation for the selected characters for the taxa. Values obtained from the population samples and the herbarium specimens were used to construct a hybrid index and pictorialized scatter diagrams.

The following six characters were employed in constructing the hybrid index: lamina width/length ratio, petiole length, angle of the lamina base, nut length, nut diameter and peduncle length. The numbers 0, 1 and 2 were assigned to represent character values of *Quercus bicolor,* intermediates and *Q. muehlenbergii* × *prinoides* respectively. A hybrid index value for individuals of the population was produced by summing the number of characters occurring in each category according to its assigned value. Thus, an individual of *Q. bicolor* on this index would receive an index value of 0, intermediates a score of 6 and those of *Q. muehlenbergii* × *prinoides* scores of 12. Character values utilized in constructing the hybrid index are presented in Table 1. The character number of lobes was not used in constructing the hybrid index, but was useful in distinguishing *Q. muehlenbergii* and *Q. prinoides.*

Table 1.

Principal morphological features and their values used in distinguishing Quercus bicolor and Q. muehlenbergii X prinoides.

Character	*Q. bicolor*	*Q. muehlenbergii* × *prinoides*
Lamina width/length ratio	0.57–0.90	0.20–0.45
Petiole length	3.0–1.2 cm.	1.7–3.0 cm.
Peduncle length	3.0–8.0 cm.	0.0–2.0 cm.
Angle of the lamina base	11°–17°	25°–45°
Nut length	2.0–3.5 cm.	1.0–1.5 cm.
Nut diameter	1.5–2.0 cm.	0.75–1.2 cm.

RESULTS

Investigation of the site confirmed suspicion of the hybrid parentage because the suspected hybrids and associated oak species on the site are quite well isolated from other oak populations. There is a small grove of post oaks (*Quercus stellata* Wang.) about 400 meters to the northwest, but they are presumably out of effective pollination range (Hardin, 1975). Many of the suspected hybrids possessed peduncles as long as 3.0 cm. or longer, and it is logical to suspect the swamp white oak as one parent as this feature is considered diagnostic for the species (MacKenzie, 1902; Deam, 1940; Steyermark, 1963). The chinquapin oak was a likely candidate for the other parent because of its presence on the site and because several of the hybrid acorns conformed in shape and dimensions to those of that species.

In order to determine whether the observed variation may have been a consequence of hybridization, the plants were compared with the suspected parents by constructing scatter diagrams using values obtained from their morphological features. Comparisons were made with values obtained from herbarium material for *Quercus bicolor* and *Q. muehlenbergii,* and the characters of lamina length, lamina width, nut length and nut diameter for several of the hybrids had values for one or more of these which were less

than the same characters of either suspected parental taxon. Hybrid character values surpassing the lower limit of variation for both *Q. bicolor* and *Q. muehlenbergii* were considered extreme. The limits used to distinguish typical from extreme variation were those of the species having the lowest value for a character. Thus, for nut length *Q. bicolor* varies from 2.0 cm. to 3.0 cm. and *Q. muehlenbergii* from 1.5 cm. to 2.0 cm. Variation among the hybrids was considered to be extreme for any individual having acorns less than 1.5 cm. in length. Of the eight individuals having extreme character values, five possess only one feature, two individuals display two features and one demonstrates smaller values for all four characters. Table 2 summarizes the occurrence of extreme variation for the eight members.

For two years prior to and following the discovery of the hybrid site, the two chinquapin species have been the subject of extensive examination in western Missouri. Population sampling has yielded quantitative data in support of a morphological characterization

Table 2.

Occurrence of extreme character values among eight members of the hybrid population.

	Lamina		Nut	
Specimen Number	length < 11.0 cm.	width < 5.0 cm.	length < 1.5 cm.	diameter < 1.2 cm.
74–150	X			
74–152	X			
74–153	X	X	X	X
74–154		X	X	
74–156		X		
74–157	X			
74–161	X		X	
74–166	X			

based on an examination of 15 populations (6 of the shrub and 9 of the tree) and 331 specimens collected from them. More recently the study has expanded to include populations in Illinois, Iowa, Nebraska, Kansas, Oklahoma, Texas and New Mexico. Although there seems to be much hybridization and introgression between them, typical members of each taxon may be distinguished on the basis of growth habit, length and width of the lamina, length and diameter of the acorn and number of lobes on one side of the lamina (Table 3). Populations of *Quercus muehlenbergii* in western Missouri differ most clearly in leaf features which vary continuously from typical *Q. prinoides* to typical *Q. muehlenbergii* with respect to length but are narrower. Leaves vary from 6.0 cm. to 18.0 cm. in length but from 2.5 cm. to 7.0 cm. in width. By comparison, typical *Q. muehlenbergii* ranges from 12.0 cm. to 20.0 cm. in length and 5.0 cm. to 9.0 cm. in width. *Quercus prinoides* varies from 4.0–10.0 cm. in length and 2.0–5.0 cm. in width. "Typical" means the leaves conform to descriptions provided by the authors of the taxa and determinations of herbarium specimens by competent botanists.

Figure 2 depicts lamina length and width values from a representative population of *Quercus muehlenbergii* occurring approximately 40 kilometers to the west of the hybrid location in adjacent Jackson County, Missouri. The same attributes scored from her-

Table 3.

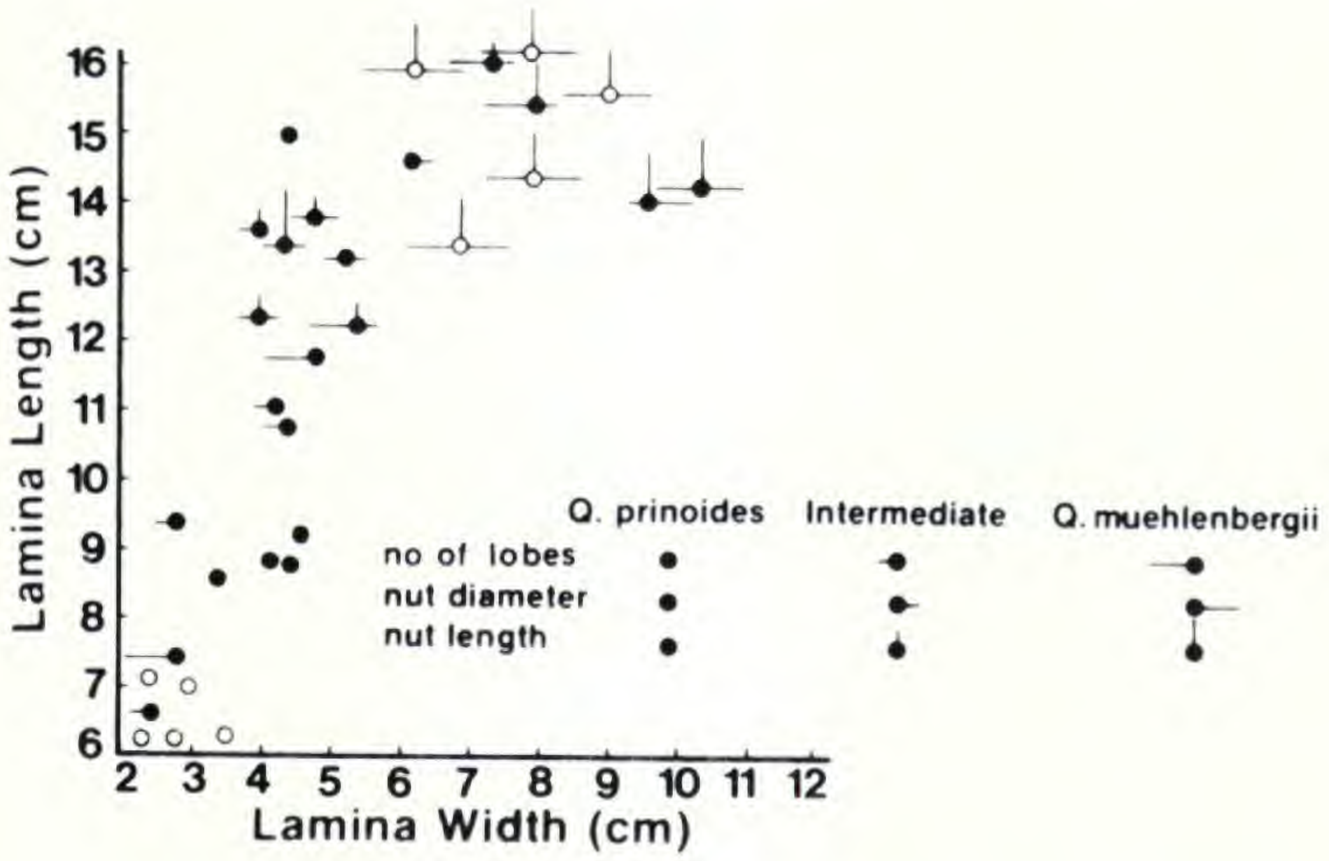
Principal morphological features and their values used in distinguishing Quercus muehlenbergii and Q. prinoides.

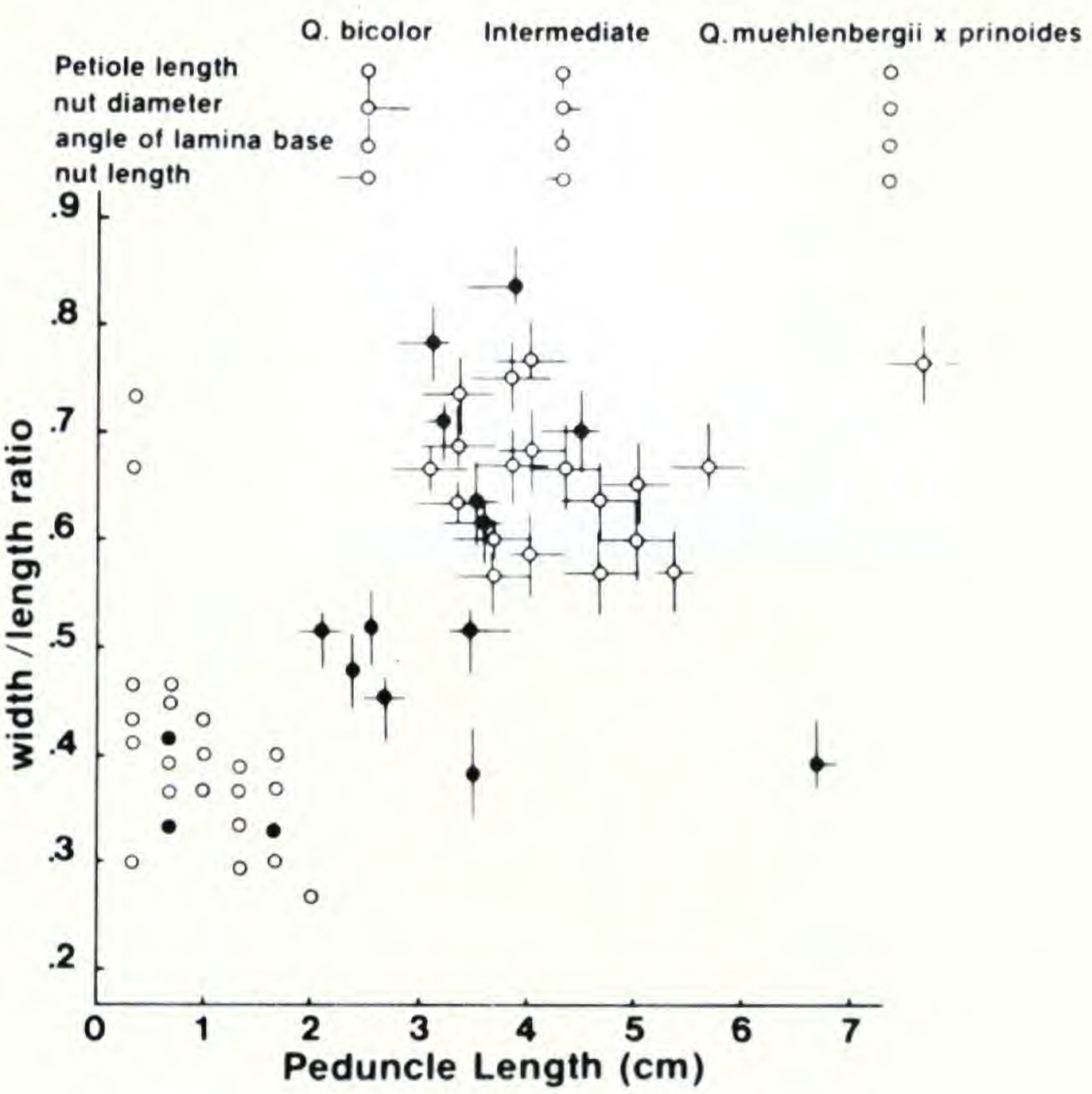
Character	Q. muehlenbergii	Q. prinoides
Lamina length	12.0–20.0 cm.	4.0–10.0 cm.
Lamina width	5.0–9.0 cm.	2.0–5.0 cm.
Number of lobes	9–12	3–7
Nut length	1.5–2.0 cm.	0.5–1.4 cm.
Nut diameter	1.2–1.8 cm.	0.5–1.0 cm.
Growth habit	medium to large tree	shrub or small tree

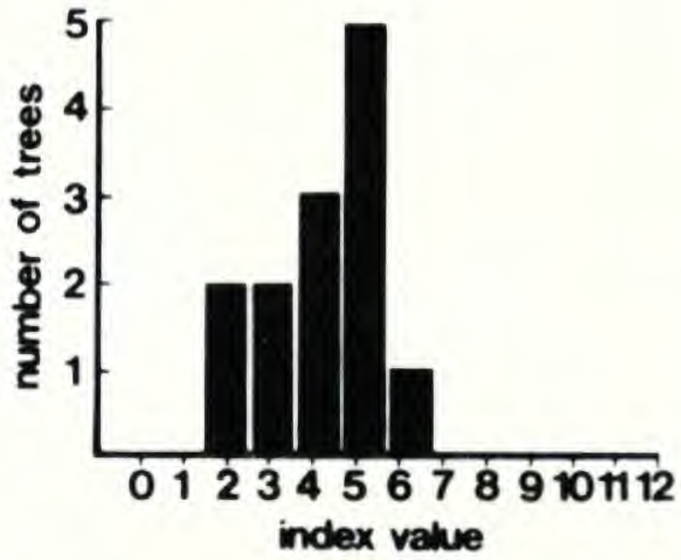
barium material of a few individuals of *Q. prinoides* and *Q. muehlenbergii* have been added as open circles. The characters have been pictorialized to include number of lobes, nut length and nut diameter. Thus five characters are represented for each individual. Plants of the population are all tree-sized individuals but the graphic pattern seems to suggest an influence by the shrub. Leaves vary in length from typical *Q. prinoides* to typical *Q. muehlenbergii,* but the majority are less than 6.0 cm. in width. Nut length varies in a manner similar to lamina length, but nut diameter conforms more to *Q. prinoides* values. Number of lobes is mainly less than 9, again a feature more typical of the shrub. The features tend to co-vary but not absolutely, a pattern suggestive of plants displaying introgressive hybridization as described by Anderson (1949).

While the variation present in chinquapin oak populations is not the subject of this paper, it may bear directly upon the observation of extreme character variation in the hybrid population. At the site three narrow-leaved individuals of *Quercus muehlenbergii* are present together with the putative hybrids and occupy a position near the top of the slope above them. Consequently, pictorialized scatter diagrams were prepared using values from the Jackson County population of *Q. muehlenbergii* introgressed by *Q. prinoides.* Because of the wide range of variation in leaf dimensions ratios were used for those features rather than their absolute values. Thus, when leaf shape, expressed as a width/length ratio, is compared to peduncle length for introgressed *Q. muehlenbergii* and *Q. bicolor,* distinction of the hybrids is more readily observable (Figure 3). The three individuals of *Q. muehlenbergii* × *prinoides* from the hybrid site were scored and are included as solid circles among the members of the population. The remaining closed circles of Figure 3 represent the members of the hybrid population.

Seven of the hybrids appear intermediate between *Quercus muehlenbergii* × *prinoides* with respect to leaf shape and peduncle length, and six conform more to values for the swamp white oak. Included as metroglyphs in Figure 3 are the characters of petiole length, nut diameter, angle of the leaf base and nut length. For the first of these, two of the hybrids have intermediate values, ten *Q. bicolor* values and one *Q. muehlenbergii* × *prinoides* value. Five of the hybrids have acorns conforming to *Q. muehlenbergii* × *prinoides* in width, seven are intermediate and one has acorns more typical of *Q. bicolor.* For the feature of nut length, four are like







Figures 2–4. 2 (top), analysis of variation for *Quercus muehlenbergii* introgressed by *Q. prinoides;* 3 (center), analysis of variation of *Q.* × *introgressa;* 4 (bottom), hybrid index for the hybrid population.

Q. bicolor, five are intermediate, and four have *Q. muehlenbergii* × *prinoides* values. Five hybrids have intermediate lamina base angles while eight are like *Q. bicolor.* The analysis of variation presented here would seem to support interpretation of the population as one of hybrid origin. However, the occurrence of characters as described above would suggest that the population members are not all first generation hybrids. Individuals intermediate in the scatter diagram have hybrid index values of 6, 5, 5, 5, 5, 5 and 4 while the remaining six have values of 4, 4, 3, 3, 2 and 2. Hybrid index values for the population are presented graphically in Figure 4.

DISCUSSION

The hybridization described here differs from other cases described in *Quercus* in the past inasmuch as three taxa are believed to be involved. Participation of a third taxon (*Quercus prinoides*) has resulted in production of individuals with variations for some characters which exceed those of the parents. Although the nature of that variation is recognizable here as diminutive features among the hybrids, this certainly would not always be the result of an influence by a third species. Of course, other explanations may be offered for the occurrence of excessively large or small features. Tucker (1970), in discussing extreme character variation in hybrid populations of *Q. gambelii* and *Q. havardii,* concluded that transgressive segregation was more likely responsible for small leaf size than the influence of a third species (*Q. turbinella*) because the hybrids exceeded all three taxa in another characteristic, foliar pubescence. This factor does not seem to apply in *Q.* × *introgressa,* as none of the extreme character values exceed typical *Q. prinoides.* It is more probable that genetic combinations which have led to diminutive variation in some of the hybrids have come to them via hybridization with tree-sized chinquapins introgressed by the dwarf.

A peripheral question concerns the status of the two chinquapin oaks. Their existence as distinct species has been called into question in recent years by Steyermark (1957, 1963), Gleason and Cronquist (1963), Stephens (1973), Hardin (1975) and historically by others (Britton, 1886; Farwell, 1923; Camp, 1934). Extensive studies of both taxa by Steyermark during preparation of the *Flora of Missouri* (1963) led him to discount the coexistence of the taxa at the specific level as his inspection found them to be varying con-

tinuously in many characters across a wide range of habitats where the two are sympatric. Therefore, he recognized a single species, *Quercus prinoides* Willd. and followed Gleason's treatment (1952) in separating the former species at the varietal level, i.e., *Q. prinoides* Willd. as *Q. prinoides* var. *prinoides* and *Q. muehlenbergii* Engelm. as *Q. prinoides* var. *acuminata* (Michx.) Gl. Steyermark (1957) further separated the latter variety into narrow and broad leaved forms, forma *acuminata* and forma *alexanderi.*

In contrast, Stephens (1973) in his *Woody Plants of the North Central Plains* maintains the taxa as distinct species but describes their intergradation on intermediate sites. He states, "The species are seen to intergrade along slopes of hills in eastern Kansas with *Quercus muehlenbergii* occupying the upper slopes, *Q. prinoides* the lower slopes and intermediates on the mid-slopes." Fernald (1970), in *Gray's Manual of Botany* also separates the plants at the specific level.

Although it is not the purpose of this report to support either of the interpretations summarized above, a nomenclatural point should be made that *Quercus* × *introgressa* is equivalent to *Q. prinoides* var. *acuminata* × *Q. bicolor* if *Q. muehlenbergii* is considered a variety. This too is undescribed.

As to the status of *Quercus* × *introgressa,* it would seem to be a mixture of F_1 and/or F_2 hybrids and backcrosses to *Q. bicolor.* The term hybrid swarm would be appropriate.

Finally, the following key is offered as a guide to the recognition of the taxa important to this study.

KEY TO QUERCUS × INTROGRESSA AND RELATED TAXA

1. Peduncles exceeding the petioles in length by twice or more. . . . . 2.
   2. Leaves twice as long as wide, fruit small (1.5 cm. × 1.0 cm.) and longer than wide. . . . . *Q.* × *introgressa.*
   2. Leaves less than twice as long as wide, fruit larger (2.5 cm. long × 1.5 cm. wide). . . . . *Q. bicolor.*

1. Peduncles up to but not exceeding the petioles in length. . . . . 3.
   3. Trees with leaves 6.0–18.0 cm. in length and 4.0–9.0 cm. wide or wider with 6–11 shallow lobes on a side each containing one principal vein and terminating in a mucronate tip. . . . . 4.
      4. Leaves 1½–2 times longer than broad with 6–10 lobes. . . . . *Q. muehlenbergii* × *prinoides.*
      4. Leaves less than 1½ times as long as broad, lobes 9–12. . . *Q. muehlenbergii.*
   3. Shrubs with leaves 4.0–8.0 cm. in length, 2.5–5.0 cm. in width, lobes 3–7. . . . . *Q. prinoides.*

ACKNOWLEDGMENTS

I would like to express my appreciation to Dr. John Dwyer of the Missouri Botanical Garden for his help with the Latin description and for his hospitality during my many visits to the herbarium while preparing the results of this study. Also, I thank Dr. Robert H. Mohlenbrock, Chairman of the Department of Botany of Southern Illinois University at Carbondale for his continuous support and encouragement of my work.

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DEPARTMENT OF LIFE SCIENCES
PENN VALLEY COMMUNITY COLLEGE
3201 SOUTHWEST TRAFFICWAY
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NOTICE OF PUBLICATION

The Hope Farm Press has announced publication of *The Forests of the Catskill Mountains, New York* by Dr. Robert P. McIntosh. This twenty-seven page treatment includes fifteen tables, five figures, a bibliography, and discussion of the history of the Catskill Mountain forest, surveyor records, tree composition, selected forest stands, spruce-fir forests, and deciduous forests. Copies of this work at $3.50 each may be obtained by writing to Charles E. Dornbusch, The Hope Farm Press, Strong Road, Cornwallville, New York 12418.

Vol. 79, No. 818 including pages 169–317, was issued June 3, 1977.

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RHODORA **July, 1977** **Vol. 79, No. 819**

CONTENTS

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Vol. 79 October, 1977 No. 820

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Rhodora

JOURNAL OF THE
NEW ENGLAND BOTANICAL CLUB

Vol. 79 October, 1977 No. 820

MONOGRAPH OF THE GENUS TIQUILIA (COLDENIA, SENSU LATO), BORAGINACEAE: EHRETIOIDEAE[1]

ALFRED T. RICHARDSON

The genus *Tiquilia* comprises 28 taxa representing 27 species and two varieties distributed among seven sections and two subgenera. The taxa occur in the deserts of North America and South America. One species, *T. nuttallii,* occurs on both continents. Most of the species are woody; all are perennials, but some are facultative annuals.

In this treatment, *Coldenia* L. sensu A. Gray is recognized as comprising two separate genera. *Coldenia* L. is treated as a monotypic genus from southern Asia, and the genus *Tiquilia* Persoon is reinstated to accommodate the taxa occurring in xeric regions of the New World. This is the first comprehensive study of *Coldenia* and *Tiquilia.* Gray's (1862) revision treated only eight species; later studies by Johnston (1924) and Howell (1937) were fragmentary.

The conclusions here are based primarily on data from morphological, chromosomal, and ecological studies, and extensive field work. Approximately 4,000 herbarium specimens representing nearly 2,500 collections were examined. The most useful morphological characters were determined to be leaf size, shape, venation, and pubescence; calyx size and pubescence; corolla color, size, pubescence, and appendages; stamen position and length; style attachment and length; and nutlet size, shape, color, ornamentation, and attachment scar.

[1]Submitted to the Graduate School of the University of Texas at Austin in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Similarities of characters, such as corolla appendages or nutlet shape and ornamentation, are not always interpreted as indicating a common origin of two or more taxa. In some cases, after consideration of the total character complement, the similarities are believed to be a result of parallel evolution under similar environmental conditions.

Morphological terms used are as defined by Stearn (1966). Unusual terms, or terms for which there is some disagreement, are defined below, and illustrated in Figure 1.

Colliculate — covered with rounded projections.

Hemi-ovoid — the result of a median longitudinal division of an ovoid figure, giving two hemi-ovoid halves.

Lanceolate — narrowly elliptic.

Pusticulate — having rounded projections.

Tuberculate — having elongate or rod-shaped projections.

Most taxa were observed in the field, although the proximity of the Chihuahuan Desert made possible more thorough observations of taxa in that region during several seasons. By contrast, only one field trip was made to the Sonoran Desert, in the summer of 1971, and field observations of the South American taxa were limited to January through June, 1973. Unusual rains in South America gave growth to abnormal vegetation in some places during that period; therefore, the observations made in these localities, while useful, had to be tempered by observations of other workers, in particular, A. Weberbauer (1936). No personal field work was done in the Galapagos Islands.

A list of *Coldenia* and *Tiquilia* specimens examined is on file at TEX.

ACKNOWLEDGMENTS

To B. L. Turner, who recommended this problem and continually encouraged me, especially during the field studies in South America, I am most grateful. My profound thanks go to M. C. Johnston for his ready counsel and his generosity in preparing the Latin diagnoses of taxa.

I am pleased to acknowledge the help of H. C. Bold, T. Delevoryas, and V. Grant for critically perusing the manuscript and offering valuable suggestions.

Credits for some of the drawings go to Steve Chase and the late Geza Knipfer, and I am particularly indebted to the latter for

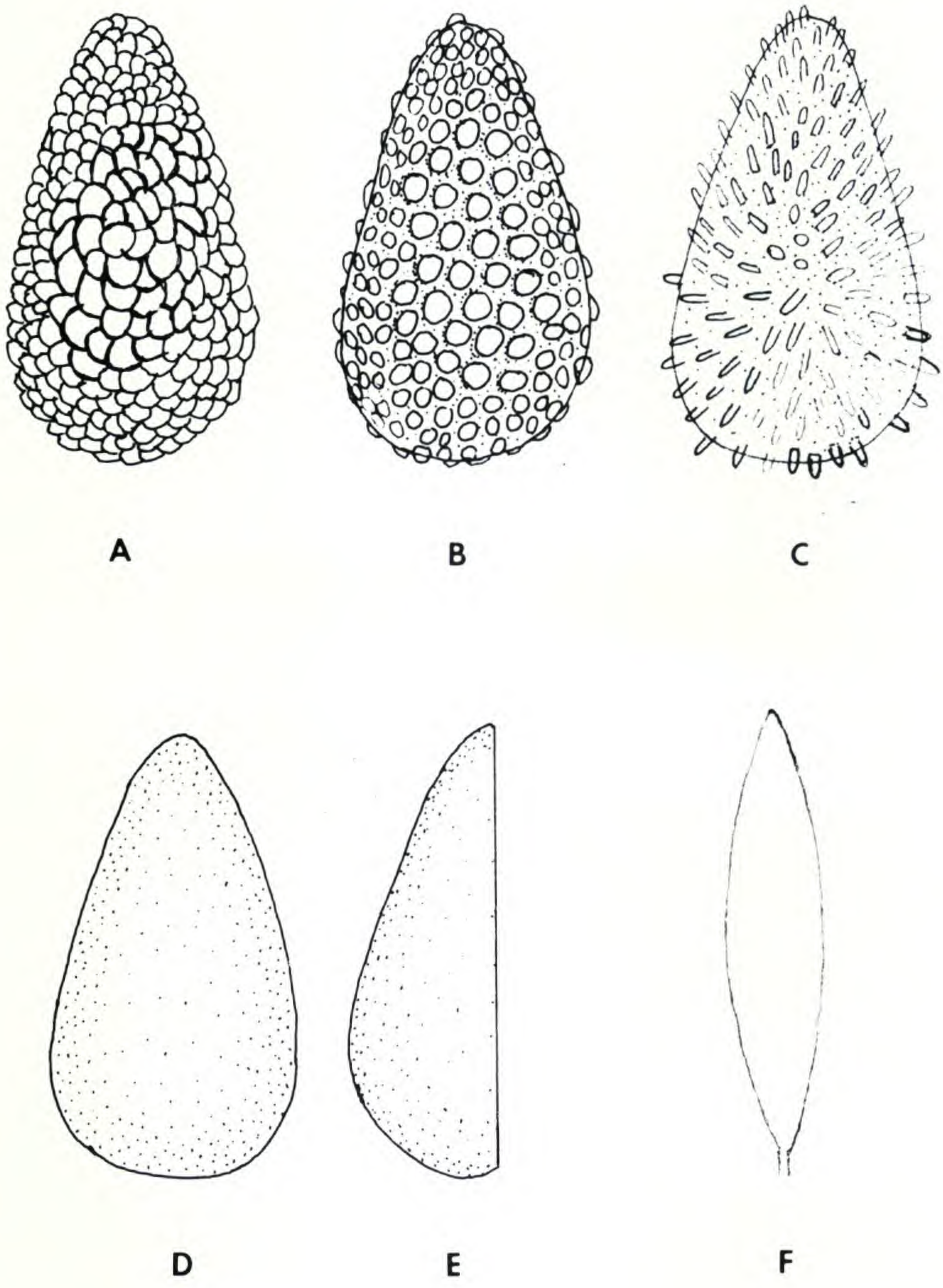

Figure 1. Illustrations of special terms. A, colliculate; B, pusticulate; C, tuberculate; D, hemi-ovoid (dorsal view); E, hemi-ovoid (lateral view); F, lanceolate.

showing me the techniques and encouraging me to proceed on my own. John Bacon, Sam Sikes, and Lowell Urbatsch offered helpful suggestions, and assistance in laboratory procedures.

For their kindnesses and valuable assistance during my term of field work in South America, I wish to thank Drs. R. Ferreyra of Lima; C. Muñoz and M. Muñoz of Santiago; A. Ruiz-Leal and F. Roig of Mendoza; A. Segástegui of Trujillo; C. Vargas and E. Carrillo of Cuzco; and N. Zambrano of Arequipa.

Grants from the National Science Foundation and the Society of the Sigma Xi provided funds for field work in South America and in Mexico.

I also thank the curators of the following herbaria from which specimens were borrowed:

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ARIZ	University of Arizona, Tucson.
B	Botanisches Museum, Berlin.
BA	Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" e Instituto Nacional de Investigaciones de las Ciencias Naturales, Buenos Aires.
BKL	Brooklyn Botanic Garden, Brooklyn.
CAS	California Academy of Sciences, San Francisco.
F	Field Museum of Natural History, Chicago.
FHO	Forest Herbarium, Oxford.
GH	Gray Herbarium, Cambridge.
HBG	Staatsinstitut für Allgemeine Botanik und Botanischer Garten, Hamburg.
JEPS	Jepson Herbarium, Berkeley.
K	Royal Botanic Gardens, Kew.
LISU	Museu, Laboratório e Jardim Botânico, Lisboa.
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TEX	The University of Texas Herbarium, Austin.
UC	Herbarium of the University of California, Berkeley.
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TAXONOMIC HISTORY

The genus *Coldenia* was described by Linnaeus (1753) and named to honor Cadwallader Colden, a correspondent of Linnaeus and then Lieutenant-governor of the colony of New York (Gray, 1888). A single Old World species, *C. procumbens,* was treated.

Ruiz and Pavon (1799) described *Lithospermum dichotomum,* which they collected in Peru, and subsequently, Persoon (1805) established the genus *Tiquilia* to accommodate this taxon, the generic name being derived from the vernacular name, reported by Ruiz and Pavon (1799) as "Tiquil-tiquil". It is possible that the cited vernacular name is simply a corruption of the Quechua word for flower, "t'ika" (Pers. comm., Helen Barler, April, 1975; Lira, 1973).

Rafinesque (1836) contributed a superfluous generic name, *Monomesia,* based on an unnamed specimen collected by Dombey which had been described in passing by Jussieu (1789) as a possible congener of *Coldenia.* J. D. Hooker (1847) described the genus *Galapagoa* in his treatment of two new species from the Galapagos Islands, and Torrey and Gray (1857), working with specimens collected on an expedition to determine a railroad route from the Mississippi River to the Pacific Ocean, described three monotypic genera, viz. *Eddya, Ptilocalyx,* and *Stegnocarpus.*

The first revisionary treatment of the genus was published as a footnote in a paper on an unrelated subject by Gray (1862). Dealing with only eight species, he combined *Eddya, Ptilocalyx, Stegnocarpus,* and *Tiquilia* with *Coldenia,* but noted, "Those who regard the reduction here foreshadowed as too great, might be better satisfied with three genera, viz. *Coldenia, Ptilocalyx,* and *Tiquilia.*" Five sections were recognized: *Eucoldenia* (*Coldenia procumbens*); *Stegnocarpus* (*C. canescens, C. greggii*); *Eddya* (*C. hispidissima*); *Tiquilia* (*C. dichotoma, C. darwinii, C. fusca*); and *Tiquiliopsis* (*C. nuttallii*).

Bentham and Hooker (1876) and Gürke (1891) followed Gray's broader circumscription of *Coldenia.* Heller (1906), however, evidently preferring a narrower circumscription of the genus, transferred *Coldenia nuttallii* Benth. ex Hook. to a new genus, *Tiquiliopsis.*

Johnston (1924), in a revisionary treatment of *Coldenia,* followed Gray but recognized only three of Gray's sections: *Eucoldenia,*

Table 1. **Classification of Coldenia Summarized from I. M. Johnston.**

Section **Eucoldenia** DC.
Series COLDENIA
C. procumbens L.
"Series" STEGNOCARPUS DC. (sic.)
C. canescens DC.
C. greggii (Torrey & Gray) Gray
"Series" TIQUILIA Gray (sic.)
C. dichotoma (Persoon) Gray
C. grandiflora Phil.
Section **Eddya** Gray
C. darwinii (Hooker f.) Gray
C. paronychioides Phil.
C. hispidissima (Torrey & Gray) Gray
C. tomentosa Watson
C. mexicana Watson
C. purpusii Brandeg.
C. cuspidata I. M. Johnston
Section **Sphaerocarya** I. M. Johnston
C. litoralis Phil.
C. atacamensis Phil.
C. parviflora Phil.
Section **Tiquiliopsis** Gray
C. nuttallii Bentham
C. palmeri Gray
C. plicata (Torrey) Coville

Eddya, and *Tiquiliopsis.* Sects. *Stegnocarpus* and *Tiquilia* were reduced to series of sect. *Eucoldenia.* Another section, *Sphaerocarya,* was designated to accommodate the taxa with spheroidal nutlets. Limiting his treatment to morphological evidence, Johnston interpreted similarity of critical characters, such as nutlet shape and presence or absence of corolla appendages, as an indication of phyletic relationships. He treated disjunct and sympatric taxa without regard to their geography, producing a confused phyletic scheme. His treatment is summarized in Table 1.

Howell (1937), in a treatment of the coldenias from the Galapagos Islands, also followed Gray's generic disposition. Most recent publications, such as floras, descriptions of new species, or clarification of established species, have followed Gray, establishing a single genus encompassing the Old World and New World taxa.

The major deviation of the present treatment from that of Gray (1862) and Johnston (1924) is the separation of the Old World and New World taxa into two genera; these genera are compared in the section on generic relationships. In addition, there is some intersectional rearrangement, and a significant number of species has been added. *Coldenia* L. is treated as a monotypic Old World genus, and *Tiquilia* Persoon is reinstated to accommodate the New World taxa. *Tiquilia* is divided into two subgenera and seven sections. Keys and descriptions are included in the section on taxonomy. The proposed classification is given in Table 2.

GENERIC RELATIONSHIPS

Coldenia sensu Gray (1862) historically has been treated as a member of subfam. Ehretioideae by various workers (Bentham & Hooker, 1876; Gürke, 1891; Johnston, 1951). The once-cleft style, its generally apical position on the fruit, and the two stigmas not differentiated into sterile and receptive tissue have served as the principal key characters relating it with this subfamily. A key to the subfamilies of the Boraginaceae, modified from Johnston (1951), is presented below.

KEY TO THE SUBFAMILIES OF BORAGINACEAE

a. Style twice forked, the 4 branches each bearing a stigma; cotyledons plicate. ..... Cordioideae.

a. Style simple or once divided; stigmas 1 or 2; cotyledons not plicate. ..... b.

b. Style borne directly on the fruit, seated terminally in its pericarp, falling away with it; style simple or once divided; endosperm usually present though often meager. ..... c.

b. Style not borne directly on the fruit, seated independently at the middle of the floral receptacle or gynobase, arising between the nutlets and free from them; style simple; stigma simple or rarely 2-lobed; endosperm usually absent; mostly herbs. ..... Boraginoideae.

c. Style usually lobed or parted; stigmas usually 2, small, capitate or elongate or rarely sub-peltate, not differentiated into receptive and sterile tissue. ..... Ehretioideae.

c. Style simple or none; stigma single, partially sterile, conic or frustrum-like or rarely peltate, stigmatic only in a sharply delimited, usually tumid circumferential band at the base, or rarely irregularly globose and broadly and somewhat indefinitely stigmatic laterally but sterile at the apex; sterile portion of stigma frequently bilobed. ..... Heliotropioideae.

Table 2. **Classification of Tiquilia.**

Subgenus **Eddya** subg. nov. TYPE: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Folia margine integra; petioli breves elliptico-rectangulares vel filiformes. Mericarpia ovata vel obpyriformia vel fructus sphaeroideus mericarpiis 4, cicatricibus stylorum apicalibus. Chromosomatum numerus basalis $x = 9$.

Section STEGNOCARPUS (DC.) A. Richardson, comb. nov.

T. canescens (DC.) A. Richardson

var. *canescens*

var. *pulchella* (I. M. Johnston) A. Richardson

Section PTILOCALYX A. Richardson, sect. nov.

Frutices erecti ad 1.0 m. alti. Inflorescentia terminalia bracteata globosa. Calyces plumosi decidui. Fructus mericarpio solitario in calyce remanenti.

T. greggii (Torrey & Gray) A. Richardson

Section EDDYA Gray

T. latior (I. M. Johnston) A. Richardson

T. hispidissima (Torrey & Gray) A. Richardson (Type)

T. turneri A. Richardson

T. tuberculata A. Richardson

T. mexicana (Watson) A. Richardson

T. gossypina (Wooton & Standley) A. Richardson

T. purpusii (Brandeg.) A. Richardson

Subgenus **Tiquilia** TYPE: *Tiquilia dichotoma* Persoon

Section TIQUILIOPSIS (Gray) A. Richardson, comb. nov.

T. nuttallii (Bentham) A. Richardson (Type)

T. plicata (Torrey) A. Richardson

T. cuspidata (I. M. Johnston) A. Richardson

T. palmeri (Gray) A. Richardson

Section TIQUILIA

T. dichotoma Persoon (Type)

T. simulans (I. M. Johnston) A. Richardson

T. grandiflora (Phil.) A. Richardson

T. ferreyrae (I. M. Johnston) A. Richardson

Section SPHAEROCARYA (I. M. Johnston) A. Richardson, comb. nov.

T. atacamensis (Phil.) A. Richardson

T. tacnensis A. Richardson

T. litoralis (Phil.) A. Richardson (Type)

T. elongata (Rusby) A. Richardson

T. hunteri A. Richardson

T. conspicua (I. M. Johnston) A. Richardson

Section GALAPAGOA sect. nov.

Table 2 (Continued)

Laminae foliorum ovatae vel obovatae. Petioli ovato-trullati. Mericarpia ovata ventraliter ab imo ad summum affixa cicatricibus longissimis. Cicatrices stylorum apicales vel subapicales.

T. paronychioides (Phil.) A. Richardson
T. galapagoa (J. T. Howell) A. Richardson
T. nesiotica (J. T. Howell) A. Richardson
T. darwinii (Hooker f.) A. Richardson (Type)

Although *Coldenia* sensu Gray fits better with the Ehretioideae than with any other subfamily, it is strikingly atypical. Johnston (1951) noted that it was clearly a member of the Ehretioideae although the relationships are not close. The following differences exist between *Coldenia* sensu Gray and other genera of the Ehretioideae:

COLDENIA SENSU GRAY	OTHER EHRETIOIDEAE
1. Herbaceous to woody; usually prostrate, or sub-erect; 1 species erect, 1 meter tall or less.	1. Trees or erect shrubs.
2. Inflorescences crowded, or reduced to 1 or few flowers.	2. Inflorescences open, distinct scorpioid cymes.
3. Fruit dry, of 4 nutlets.	3. Fruit a drupe.

In addition to the above characteristics, style attachment and leaf venation are distinctive. In the New World taxa, style attachments are apical, subapical, sub-basal, basal, or gynobasic; this latter condition brings to mind subfam. Boraginoideae.

In taxa with lobed leaves, the lateral veins run from the midrib to the sinuses rather than to the apices of the lobes. This feature was noted by DeCandolle (1845), who found this condition duplicated only in *Crataegus oxyacantha* (Rosaceae) and in species of *Rhinanthus* (Scrophulariaceae). Johnston (1951) stated that in these two taxa only an occasional or secondary vein behaved in this manner whereas in *Coldenia* all lateral veins go to the sinuses. He described this condition as unorthodox and perhaps unique.

The present investigation confirms Johnston's conclusions regarding *Crataegus oxyacantha;* however, in the opinion of the present writer, at least four species of *Rhinanthus* (*R. crista-galli, R. greenlandicus, R. major,* and *R. minor*) duplicate the venation of *Coldenia.*

Coldenia sensu Gray separates into two genera with distinct characters and without intermediates. In a recent paper (Richardson, 1976) the New World genus *Tiquilia* Persoon is reinstated and *Coldenia* L. is recognized as a monotypic Old World genus. *Tiquilia* Persoon is comprised of perennial, usually woody plants without adventitious roots, and with symmetrical leaves and pentamerous flowers solitary or in clusters, axillary or subtended by bracts. It occupies xeric regions of the New World. *Coldenia* L. is comprised of an herbaceous annual with adventitious roots, asymmetrical leaves, and tetramerous flowers, solitary, extra-axillary, not subtended by bracts. It occupies forest and woodland riverbanks and dried rice fields of the Old World. *Coldenia* is treated below.

Coldenia L., Sp. Pl. **1:** 125. 1753.

Lobophyllum F. Mueller, Hooker's Jour. Bot. Kew Gard. Misc. **9:** 21. 1857.

Prostrate annual herbs. Leaves alternate, blades obovate, distinctly asymmetric, the margins crenate or lobed, the veins terminating at the sinus bases. Flowers solitary, sub-sessile, extra-axillary, 4-merous. Styles 2. Fruit spheroid, of 4 nutlets.

Coldenia procumbens L. Sp. Pl. **1:** 125. 1753. (Holotype: L, No. 174.1, not seen. Photograph, TEX!).

Lobophyllum tetrandrum F. Mueller, Hooker's Jour. Bot. Kew Gard. Misc. **9:** 21. 1857. TYPE: **Australia.** VICTORIA: Sturt Creek, on periodically inundated banks of rivers and streams, March 1856, *Mueller s.n.* (Holotype, K. not seen. Isotype, MEL!).

Coldenia angolensis Welw., Ann. do Cons. Ultramarino **1:** 527–592. 1859. TYPE: **Africa.** ANGOLA: Barra do Dande district near Bombo, Sept. 1858, *Welwitsch 5445* (Holotype, LISU!).

Stems branching, slender (Figure 2), 1.0–5.5 mm. thick, villous with hairs ca. 1.0 mm. long, sometimes bearing adventitious roots. Leaf blades (Figure 3A) 1.0–3.3 cm. long, 0.6–1.8 cm. across; upper surfaces with appressed straight hairs to 1.0 mm. long converging on the medians between the veins and flowing toward the margins; lower surfaces villous or with spreading hairs ca. 1.0 mm. long

Figure 2. Drawing of habit of *Coldenia procumbens*.

especially along the veins; petioles 0.2–0.9 cm. long with spreading hairs ca. 1.0 mm. long. Calyces ca. 1.5 mm. long, lobes unequal, lanceolate to ovate, joined at or near the base, with apically appressed hairs to 1.0 mm. long on inner and outer surfaces. Corollas sometimes scented, white to yellowish white, campanulate, minute, 1.3–2.0 mm. long. Stamens included, adnate to the corollas about the mid-point, alternate with the lobes; filaments ca. 0.3 mm. long. Styles united basally. Fruit (Figure 3B) spheroid, 2.2–4.8 mm. across, lobed, puberulent and spined, apical spines overtopping the styles; mericarps 4, joined into pairs by a thick ridge, a pronounced sulcus at right angles to the ridge marking the unions of the pairs, each mericarp having one large and one small commisural face (Figure 3C).

DISTRIBUTION: Mainly in southeastern and southwestern Asia, northeastern Africa, Madagascar, and northern Australia (Figure 4). *Coldenia procumbens* is commonly found growing on river banks that have been inundated, or on dried-up rice paddies. The nutlets float, making them ideally suited for dispersal by water. It is likely that much of the Old World distribution of this taxon has been brought about by man as the plants are often associated with rice fields.

Coldenia procumbens blooms throughout the year.

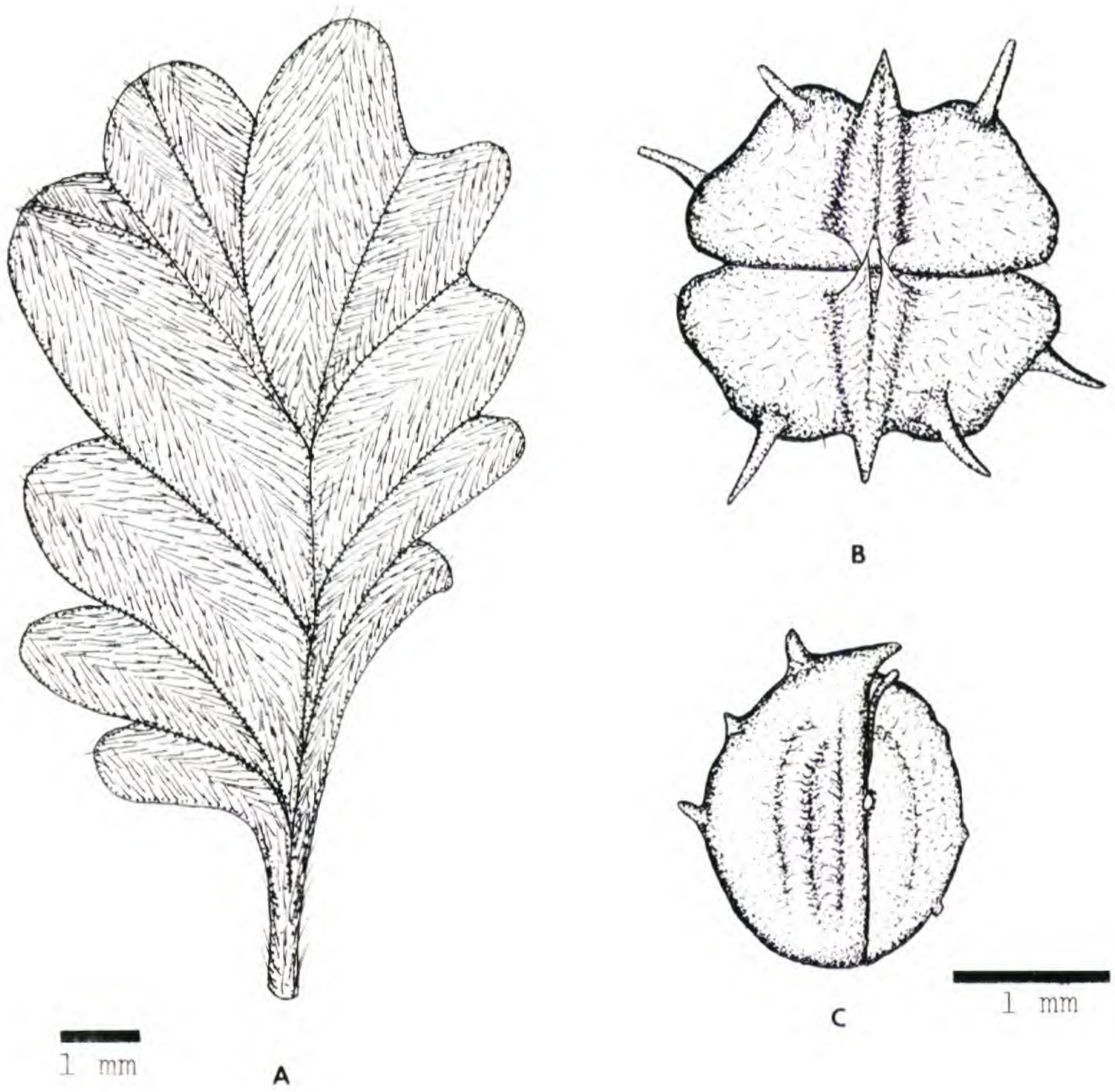

Figure 3. *Coldenia procumbens*. A, leaf; B, fruit; C, nutlet.

CHROMOSOMAL STUDIES

Little work has been done on the chromosomes of sub-fam. Ehretioideae. Chromosome counts have been reported for only three genera: *Ehretia*, *Cortesia*, and *Coldenia*. The first counts reported were by Britton (1951), for three species of *Ehretia*. He counted *E. anacua*, $2n = 40$, *E. microphylla*, $2n = 32$, and *E. thyrsiflora*, $2n = 32$. Since all the numbers are multiples of eight, he proposed $x = 8$ as the base number for the subfamily. In the same work, on the basis of counts of 90 species and varieties representing 19 genera, he proposed $x = 8$ as the base number for the Boraginaceae. Subsequently, Chuang *et al.* (1963) reported *Ehretia dicksonia* as $n = 30$; Bhattacharya (1968) reported $n = 15$ for *E. acuminata;* and Baquar and Askari (1970, 1970a) reported *E. as-*

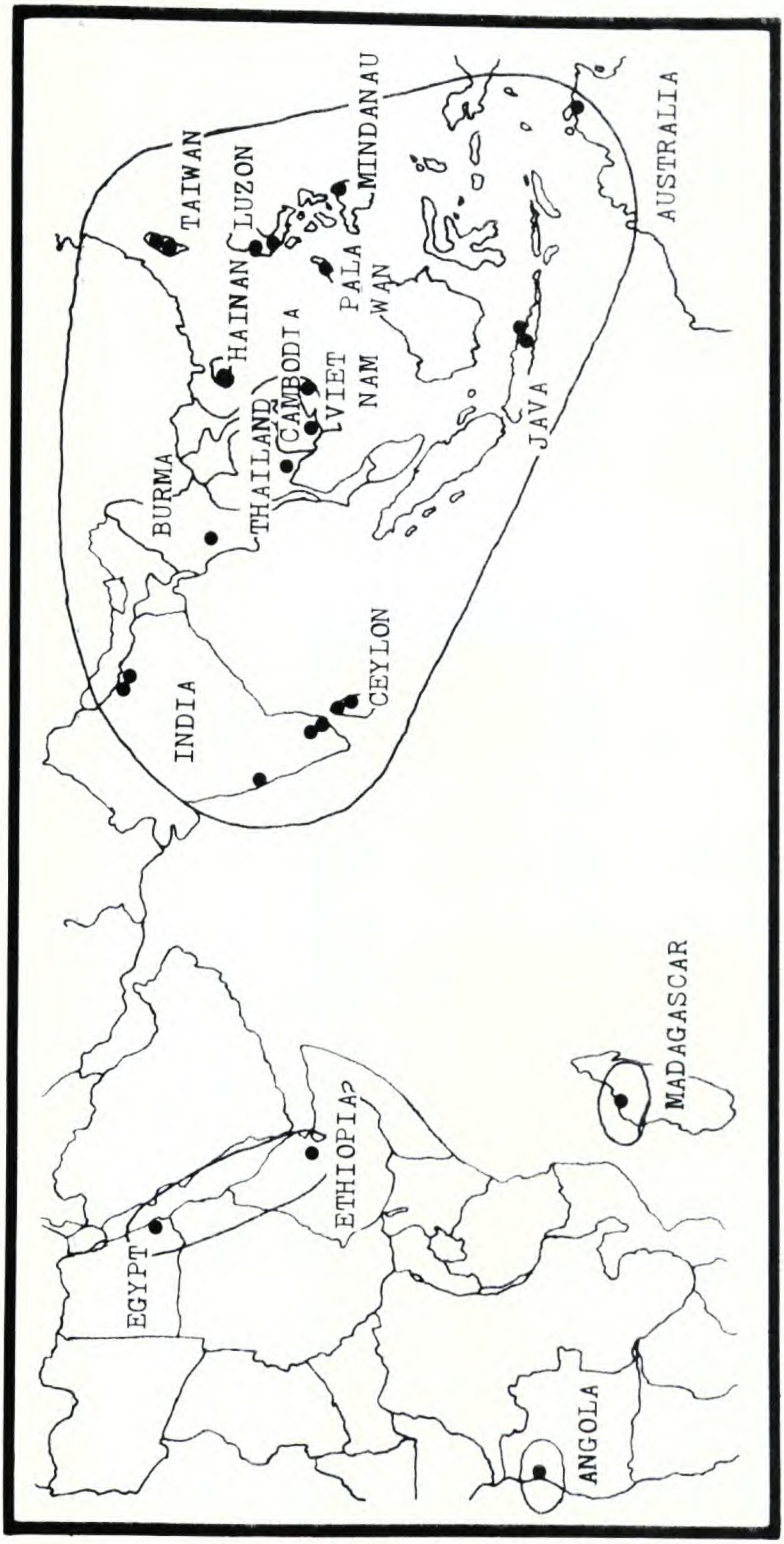

Figure 4. Distribution of *Coldenia procumbens*.

pera as $n = 8$. These counts seem to support Britton's hypothesis of a base number of $x = 8$. However, Di Fulvio (1965) found *Cortesia cuneifolia* to be $2n = 18$, suggesting the possibility of a base number of $x = 9$.

Chromosome numbers for *Coldenia* sensu lato were published by Chisaki (1959). He reported *C. canescens* and *C. purpusii* to have $n = 9$, and *C. palmeri* and *C. plicata* with $n = 8$. No further counts have been published.

During this investigation bud material was collected in the field for meiotic counts and placed in a modified Carnoy's fluid (4 parts chloroform : 3 parts absolute ethanol : 1 part glacial acetic acid), and stored in the refrigerator until the counts were made. Aceto-carmine stain was used.

A relatively low number of buds was successfully counted. The small size of the buds in the desirable stages of meiosis made necessary the use of a microscope to dissect them from the enclosing leaves, bracts, or bud clusters. Consequently, it was impossible to readily select buds of the proper size in the field; instead, actively growing, flowering sections of the plants were selected in the hope that some countable buds would be present. No correlation was noted between the time the buds were collected and the stage of meiosis. Most cells counted were in early anaphase. Counts were made for 81 populations, representing 22 of the 27 species. The results are listed in Table 3. Vouchers are deposited at TEX.

Two base numbers are readily recognized: $x = 9$ and $x = 8$. On the basis of distinctive morphology and distribution as well as chromosome number, two subgenera are recognized: Subg. *Eddya* with a base chromosome number where $x = 9$, and subg. *Tiquilia* where $x = 8$. Within subg. *Eddya,* chromosome numbers are not of taxonomic importance as all species have the same haploid number, $n = 9$. However, one aneuploid individual, $n = 8$, was growing in a population of *Tiquilia purpusii* from which a count of $n = 9$ was also made. Bud material was collected again from that population but no meiotic microsporocytes were found. Since all other populations counted had $n = 9$, that number is most likely predominant in the population. Whether the $n = 8$ count represents one aberrant individual or a number of individuals is not known. It is believed, however, that the count is accurate.

Chromosome numbers have been useful in determining relationships in subg. *Tiquilia.* The single North American section, *Tiquili-*

Table 3. **Species of Tiquilia Examined for Chromosome Number.**

Species	*n* number	Location and Voucher
Subgenus **Eddya**		
Section STEGNOCARPUS		
T. canescens var. *canescens*	9	**Arizona:** COCONINO CO. S rim of Grand Canyon. *Raven 13122*[a]*
	9	**Mexico:** COAHUILA. 17.1 mi. E of Musquiz. *Richardson 1587A.*
	9	**Mexico:** COAHUILA. Hwy. 57, 27.8 mi. S of Nuevo Rosita road. *Richardson 1589A.*
Section PTILOCALYX		
T. greggii	ca. 9	**Mexico:** CHIHUAHUA. Ca. 18 mi. S of Ojinaga. *Richardson 1472D, 1472E.*
	9	**Mexico.** CHIHUAHUA. 25.1 mi. N of Aldama. *Richardson 1602A, 1602B,* and *1602C.*
	9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1609B.*
Section EDDYA		
T. latior	9	**Arizona:** COCONINO CO. Lee's Ferry. *Sanderson 428.*
T. hispidissima	9	**New Mexico:** OTERO CO. White Sands. *Richardson 1613A, 1613B.*
	9	**Texas:** BREWSTER CO. 42.5 mi. S of Marathon. *Bacon 954.*
	9	**Mexico:** CHIHUAHUA. 11.2 mi. SE of hwy. 16 from Aldama on road to Pasado El Granjero. *Richardson 1605A, 1605B, 1605E.*
	ca. 9	**Mexico:** CHIHUAHUA. 50 mi N of Aldama. *Richardson 1606B.*
T. turneri	9	**Mexico:** COAHUILA. 12.4 mi. S, 2 mi. W of Cuatro Ciénegas. *Richardson 1595E, 1595F.*
T. mexicana	ca. 9	**Mexico:** CHIHUAHUA. Ca. 11 mi. S of Ojinaga. *Richardson 1465.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
	9	**Mexico:** COAHUILA. 33 mi. W of Saltillo. *Richardson 1572E, 1572F.*
	9	**Mexico:** COAHUILA. 18.6 mi. S of Cuatro Ciénegas. *Richardson 1598A, 1598B, 1598C.*
T. gossypina	ca. 9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1608B.*
	ca. 9	**Mexico:** CHIHUAHUA. 50 mi. N of Aldama. *Richardson 1610B.*
	ca. 9	**Mexico:** CHIHUAHUA. 137.9 mi. N of Camargo. *Richardson 1672–10, 1672–14.*
	ca. 9	**Mexico:** COAHUILA. 40 km. N of Monclova. *Richardson 1429A.*
	ca. 9	**Mexico:** COAHUILA. 4.4 mi. W of Paila. *Richardson 1577A, 1577B, 1577D.*
	9	**Mexico:** COAHUILA. 31 mi. N of San Pedro de las Colonias. *Richardson 1581A, 1581B.*
	9	**Mexico:** COAHUILA. 64.1 mi. N of San Pedro de las Colonias. *Richardson 1584A.*
	9	**Mexico:** COAHUILA. 39 km. N of Monclova. *Richardson 1593B.*
	9	**Mexico:** COAHUILA. 39 km. N of Monclova. *Richardson 1594B.*
	9	**Mexico:** COAHUILA. 65.3 mi. N of San Pedro de las Colonias. *Richardson 1652–11.*
	ca. 9	**Mexico:** COAHUILA. 36.1 mi. N of San Pedro de las Colonias. *Richardson 1656B.*
	ca. 9	**Mexico:** COAHUILA. 36.1 mi. N of San Pedro de las Colonias. *Richardson 1657E.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
T. purpusii	9	**Mexico:** NUEVO LEON. 5.5 mi. S of José Maria Aguirre. *Moran 6320*[b].
	9	**Mexico:** NUEVO LEON. 20.2 mi. N of Matehuala. *Richardson 1695B.*
	9	**Mexico:** SAN LUIS POTOSÍ. Hwy. 80, 16.6 mi. E of junction with hwy. 101. *Richardson 1525.*
	9, 8	**Mexico:** SAN LUIS POTOSÍ. Road to Guadalcazar, at junction with hwy. 57. *Richardson 1541.*
	9	**Mexico:** SAN LUIS POTOSÍ. 5 mi. N of La Ventura. *Richardson 1543A, 1543B.*
	9	**Mexico:** SAN LUIS POTOSÍ. Cerritos road, 5 mi. from junction with hwy 57. *Richardson 1551.*
	9	**Mexico:** SAN LUIS POTOSÍ. 25 mi. W of Ciudad Maiz. *Richardson 1691B, 1691C, 1691E.*
	9	**Mexico:** SAN LUIS POTOSÍ. Hwy. 57, 39.7 mi. N of intersection with hwy 80. *Richardson 1693A.*
	9	**Mexico:** TAMAULIPAS. 50 mi. SW of Victoria. *Richardson 1519.*
Subgenus **Tiquilia**		
Section TIQUILIOPSIS		
T. nuttallii	8	**California:** INYO CO. Bishop Creek. *Raven 14306*[c].
T. plicata	8	**Arizona:** YUMA CO. Yuma. *Richardson 1628.*
	8	**California:** IMPERIAL CO. Junction hwys. 80–98 and road from Ogilby. *Alava 1809*[d].
	8	**California:** IMPERIAL CO. Ca. 20 mi. E of Winterhaven. *Bacon 922A.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
	8	**California:** RIVERSIDE CO. Palm Springs. *Bacon 939A, 939B, 939D.*
	8	**California:** RIVERSIDE CO. 51.6 mi. E of 29 Palms. *Bacon 942A, 942B, 942D.*
	ca. 8	**California:** RIVERSIDE CO. 51.6 mi. E of 29 Palms. *Bacon 942C.*
	8	**California:** SAN DIEGO CO. 29 mi. W of Ocotillo. *Bacon 935A, 935B, 935C, 935D.*
	8	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937B, 937D.*
	8	**California:** SAN DIEGO CO. 12.3 mi. W of hwy. S-78 from junction of hwys. S-86 and S-78. *Bacon 938A.*
	8	**Mexico:** BAJA CALIFORNIA. 57 mi. S of Mexicali. *Bacon 923A, 923B, 923C.*
	8	**Mexico:** SONORA. Desemboque. *Richardson 1620.*
T. cuspidata	8	**Mexico:** BAJA CALIFORNIA. 70 mi. S of Mulege. *Hartman & Seaman 3266.*
	8	**Mexico:** SONORA. Km. 95 between Hermosilla and Bahia Kino. *Richardson 1616.*
T. palmeri	8	**Arizona:** YUMA CO. Yuma. *Bacon 921A, 921B, 921C.*
	8	**California:** IMPERIAL CO. Junction of hwys. 8 and S-2. *Bacon 934A, 934B.*
	9	**California:** IMPERIAL CO. Junction of hwys. 8 and S-2. *Bacon 934C.*
	8	**California:** RIVERSIDE CO. 27 mi. S of Vidal. *Alava 1831*[c].

Table 3 (Continued)

Species	*n* number	Location and Voucher
	8	**California:** RIVERSIDE CO. 35.4 mi. S of Vidal. *Bacon 944A, 944B, 944C.*
	8	**California:** SAN DIEGO CO. 8 mi. W of Ocotillo. *Bacon 936.*
	8	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937A, 937C.*
	9	**California:** SAN DIEGO CO. 1 mi. N of hwy. 76, Ocotillo road to Borrego Springs. *Bacon 937E.*
	8	**Mexico:** BAJA CALIFORNIA. 31.3 mi. S of Puertocitos. *Bacon 924A, 924C.*
	8	**Mexico:** BAJA CALIFORNIA. 39.7 mi. S of Puertocitos. *Bacon 925B, 925C.*
	8	**Mexico:** BAJA CALIFORNIA. 59 mi. S of Puertocitos. *Bacon 926B, 926C.*
	8	**Mexico:** SONORA. 20 mi. W of Sonoita. *Richardson 1622.*
	8	**Mexico:** SONORA. 95 km. W of Sonoita. *Richardson 1625A.*
Section TIQUILIA		
T. dichotoma	16	**Peru:** ICA. 383 km. S of Lima. *Richardson 2098.*
T. simulans	16	**Peru:** AREQUIPA. 129 km. N of Camaná. *Richardson 2150.*
	16	**Peru:** AREQUIPA. 2 km. E of Puerto Lomas. *Richardson 2154.*
T. grandiflora	16	**Peru:** AREQUIPA. 30 km. W of Arequipa on Cerro Verde road. *Richardson 2124.*
T. ferreyrae	16	**Peru:** AREQUIPA. 72 km. SW of Nazca. *Richardson 2100.*

Table 3 (Continued)

Species	*n* number	Location and Voucher
Section SPHAEROCARYA		
T. tacnensis	16	**Peru:** TACNA. 70 km. N of Tacna. *Richardson 2130.*
	16	**Peru:** TACNA. 51 km. n of Tacna. *Richardson 2138.*
T. elongata	ca. 16	**Peru:** AREQUIPA. 76 km. SE of Camaná. *Richardson 2112.*
	16	**Peru:** AREQUIPA. 99 km. SE of Camaná. *Richardson 2115.*
	ca. 16	**Peru:** AREQUIPA. 19 km. N of Arequipa. *Richardson 2117.*
	ca. 16	**Peru:** AREQUIPA. Yura. *Richardson 2119.*
	ca. 16	**Peru:** AREQUIPA. Outside Arequipa, slopes of Chachani. *Richardson 2120.*
T. hunteri	14	**Peru:** AREQUIPA. 714 km. S of Lima between Chala and Camaná. *Richardson 2106.*
T. litoralis	15	**Chile:** ANTOFAGASTA. Pan American hwy., near turnoff to Taltal. *Richardson 2173.*
	ca. 15	**Chile:** ATACAMA. S of Copiapó. *Richardson 2179.*
T. conspicua	16	**Peru:** AREQUIPA. Mollendo. *Richardson 2126.*
	16	**Peru:** AREQUIPA. Mollendo. *Richardson 2140.*
Section GALAPAGOA		
T. paronychioides	ca. 14–16	**Peru:** PIURA. 100 km. S of Talara. *Richardson 2050.*

*Superscript letters refer to counts made from the following sources:
[a]Cave (1959); voucher at UC.
[b]Chisaki (1959); voucher at UC.
[c]Chisaki (1960, not published); voucher at UC.
[d]Chisaki (1959); voucher at JEPS.
[e]Chisaki (1959); voucher at JEPS.

opsis, is diploid with $n = 8$. Of particular note is *Tiquilia palmeri.* Chromosome counts were made from eleven populations of this species. Nine of them were $n = 8$. The remaining two populations were found to have aneuploids. In each case, two individuals were counted $n = 8$ and one was $n = 9$. No significant corresponding morphological differences were detected between the diploids and aneuploids.

Tiquilia nuttallii, also in sect. *Tiquiliopsis,* is poorly known chromosomally. This is the only species occurring on both American continents. Only one count from North America, $n = 8$ (Chisaki, 1960), has been reported. Unfortunately no South American populations have been counted. Since specimens from the two continents are indistinguishable morphologically, and they have similar flavonoid chromatograph patterns (Richardson, 1975, unpublished), it seems likely that the chromosome numbers are the same. More counts are needed of populations from both continents.

The remaining three sections are South American in distribution, and all are polyploids, the predominant haploid number being $n = 16$. Two of the more advanced species, *Tiquilia litoralis* and *T. hunteri* (sect. *Sphaerocarya*), have derived haploid numbers of $n = 15$ and $n = 14$ respectively.

The tetraploids could have arisen by one of the following methods. (1) There was a single introduction of a tetraploid from North America. However, there are no tetraploids known from North America. (2) Diploids were introduced from North America. Subsequent doubling of the chromosome complement produced a population better adapted to the South American deserts, and the less well-adapted diploids failed to survive. This is not to imply that tetraploids are necessarily better adapted to a given habitat than diploids, although this condition has been observed (Grant, 1971, p. 248).

Whether the polyploids originated as alloploids or as autoploids is not known. Alloploids could have arisen by hybridization and subsequent doubling of the chromosome complement. Autoploids could have arisen by somatic doubling in mitosis or by nonreduction in meiosis (Grant, *op. cit.*). If the ancestral polyploids were autoploids, diploidization has occurred since (Brown & Bertke, 1969, p. 497), and so the species are properly called amphidiploids. Meiotic pairing is regular, and no multivalents have been observed.

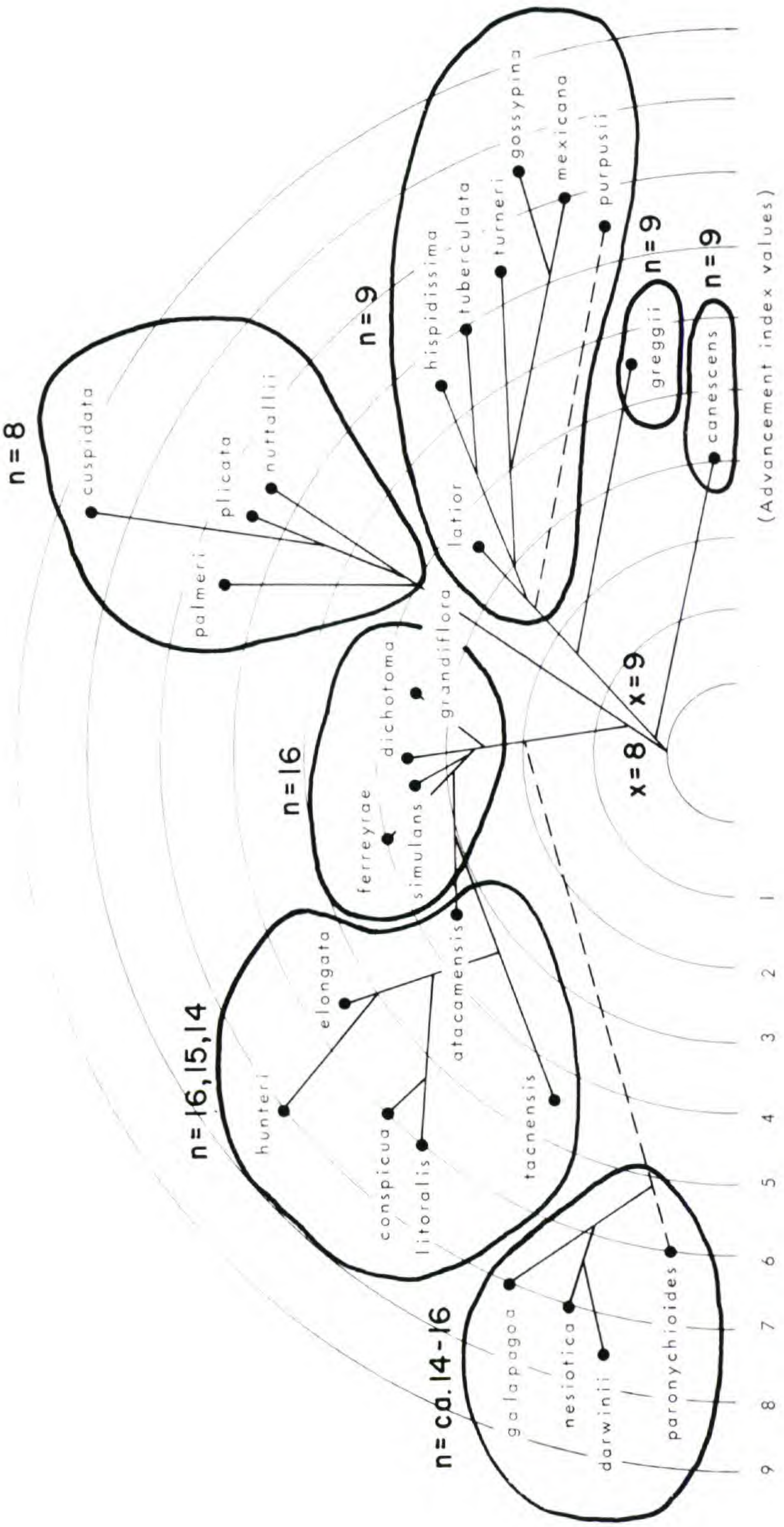

Figure 5. Diagram of species relationships and degree of advancement in *Tiquilia*.

No chromosome numbers are known for the species of sect. *Galapagoa,* excepting *Tiquilia paronychioides* which has been counted as n = ca. 14–16. Although limited in its usefulness, the information has served to identify the species as polyploid. More chromosome counts of *T. paronychioides* and the species of the Galapagos Islands are greatly desired.

ECOLOGY AND DISTRIBUTION

The taxa of *Tiquilia* are all xerophytic perennials. Most species are woody, and some are subshrubs; one species is a small erect shrub. It is important to note, however, that some species can flower and fruit in their first year, thus functioning as annuals if eliminated by subsequent adverse conditions. Such plants have the obvious appearance of herbaceous annuals; some western North American species have, in fact, been erroneously reported to be herbaceous annuals.

Humphrey (1932) examined *Tiquilia canescens,* regarding its adaptations to dry conditions. He noted the following characteristics: (1) perennial root system capable of utilizing water, which may be available for only a few hours; (2) root system with horizontal and vertical roots, allowing absorption of water from light showers as well as the less transient moisture deeper in the soil; (3) pubescence; (4) revolute leaf blade margins; (5) stomata on abaxial leaf surface; (6) reduced number of stomata per unit area; (7) little intercellular space within the leaf; (8) leaf shedding during drought; (9) osmotic pressure above that of the average mesic leaf. Other species have not been examined, but *T. canescens* can be judged as, at least partially, representative of the genus.

The species are widely distributed over the xeric regions of North America and South America. The plants are usually dominants where they grow, but they usually do not grow in close proximity to other plants, with the exception of other species of the same genus. It is not uncommon to find two, three, or even four species growing together, especially in North America. In spite of this sympatry, no hybrids have been detected.

Subg. *Eddya* includes taxa of southwestern United States and north-central and northeastern Mexico. Subg. *Tiquilia* includes taxa of western United States and Mexico, and South America. Subg. *Eddya* is distributed principally in trans-Pecos Texas, Chi-

huahua, and Coahuila, but extends south to Hidalgo, east to Tamaulipas, and north and west to central Utah and southeastern Nevada. The taxa in this subgenus are primarily adapted to gypseous ($CaSO_4$) soils. Some taxa are gypsum endemics, while others are occasionally found growing in non-gypseous soils.

Tiquilia canescens diverges from the general pattern found in subg. *Eddya* by growing in various soil types, although it is most abundant in gypseous areas. Also, it is occasionally seen growing in close proximity with other plants. With these liberations it has been able to extend its range as far west as eastern California and into Baja California.

In five species of subg. *Eddya*, viz. *Tiquilia latior*, *T. hispidissima*, *T. tuberculata*, *T. turneri*, and *T. gossypina*, there is a reduction of the inflorescence to usually one flower; a reduction in overall leaf size (excepting *T. latior*); and a pronounced decrease in leaf blade width, partially due to an increased inrolling of the margin. The leaf reductions could be an adaptation enabling the leaves to live over a longer period of drought and therefore be available to function throughout the year as sporadic showers give moisture. With few flowers being produced, a plant's resources can be concentrated to producing a small number of fruits before drought again terminates the plant's activities. An added advantage is that during a prolonged period of rain the plants flower and fruit continuously, as long as moisture is available. *Tiquilia latior* was not observed in the field; however the other species were observed at various times of the year, and they consistently bloom after rains.

In subg. *Tiquilia*, sect. *Tiquiliopsis* comprises four species limited in distribution to the western United States and Mexico, and western Argentina. *Tiquilia cuspidata* grows mainly in southern Baja California and adjacent Sonora; it is replaced by *T. palmeri* from northern Baja California to southern California and western Arizona, with only a short band of sympatry. Again with only a short band of sympatry, *T. nuttallii* continues from southern California northward to Washington, and eastward into Utah, Arizona, and western Wyoming. This species also grows in western Argentina. Unlike the other South American species, it appears to be a recent introduction. *Tiquilia plicata* is sympatric with *T. palmeri*, less so with *T. nuttallii* in southern California, and grows also in Arizona.

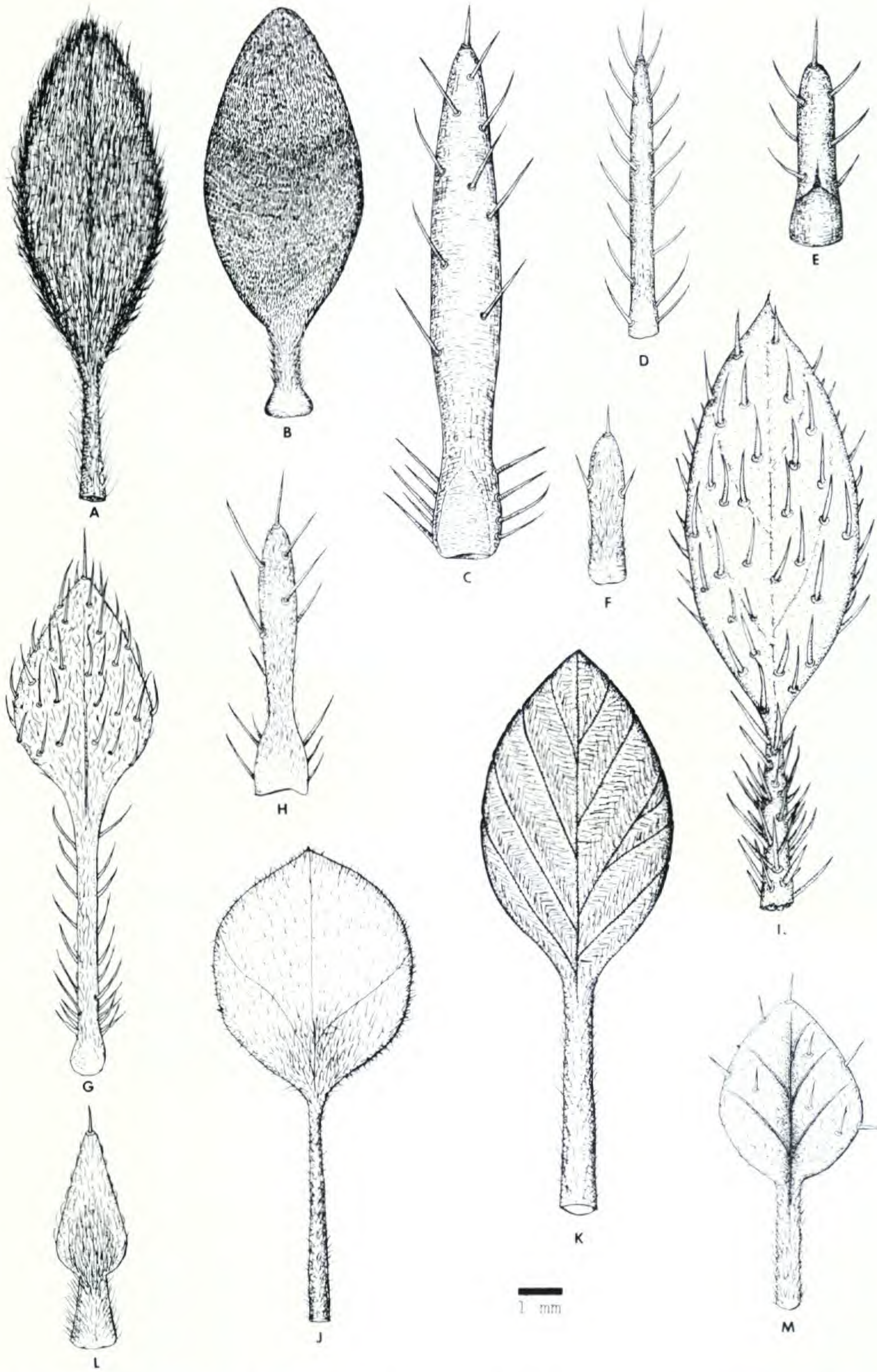

Figure 6. Drawings of leaves of *Tiquilia*. A, *T. canescens;* B, *T. greggii;* C, *T. latior;* D, *T. hispidissima;* E, *T. tuberculata;* F, *T. turneri;* G, *T. mexicana;* H, *T. gossypina;* I, *T. purpusii;* J, *T. nuttallii;* K, *T. plicata;* L, *T. cuspidata;* M, *T. palmeri.*

The species of this section grow in sand or a mixture of sand, clay, and gravel. They grow in a region with well-defined seasons of drought and rain. They have larger, broader leaves than most members of subg. *Eddya,* and differ also in producing inflorescences with clustered flowers, making them well-adapted to producing large quantities of seeds during the wet season and going dormant the remainder of the year.

The remaining three sections of subg. *Tiquilia* occur in western South America, including the Galapagos Islands. Three species, *Tiquilia atacamensis, T. elongata,* and *T. grandiflora,* have adapted to inland medium altitudes; the remainder are coastal.

The mainland species range from central Ecuador through Peru to the vicinity of Caldera and Copiapó in northern Chile. Seven species are endemic to Peru, six of them in the southern portion. One species is endemic to northern Chile; two species occur in southern Peru and northern Chile; and one species, *Tiquilia paronychioides,* occupies the total mainland distributional range of the genus. It is the most versatile South American species, even growing in close proximity to other plants in Ecuador. The three Galapagoan species are abundant on the islands, constituting a major part of the coastal flora (pers. comm., Dr. Aura Star, Oct., 1974; Wiggins & Porter, 1971).

It is not clear what ecological factors limit the distribution of the species, excepting the higher altitudes of the inland species. This factor was also observed by Johnston (1956). Essentially, all the species grow without competition in sand, which is abundant throughout the coastal and inland habitats. Species of different sections often grow together, but intrasectional sympatry is not great.

Of particular interest to South American phyto-geography is the lomas formation (Weberbauer, 1936), occurring principally in Peru and extending into northern Chile. The lomas vegetation, which receives moisture from winter and spring fogs, includes xerophytic, mesophytic, and even hydrophytic plants such as ferns, mosses, peperomias, and begonias where otherwise there would be only xeric plants, or none. The plant communities found in a lomas formation vary depending on altitude and distance from the sea, since the fogs are carried inland at consistent altitudes by the prevailing south and west winds (Weberbauer, 1936).

Tiquilia has adapted to receiving moisture from fog, and has often been collected in the lomas. I have seen populations in full bloom flourishing in locales where the inhabitants reported no rains had fallen for several months.

PHYLOGENY

Since there are no genera known to be closely related to *Tiquilia* in the New World, and no fossil evidence is reported, a hypothesized phylogeny must be inferred from present distributions, present relationships, and a knowledge of general geological and evolutionary trends. Present distributions have already been discussed.

There is no clear evidence as to whether the ancestral base chromosome number for the genus is $x = 9$ or $x = 8$. Both ascending and descending aneuploidy are known for other genera, although what appear to be descending series are more frequently encountered.

In order to express phylogenetic relationships graphically and numerically, the Wagner Divergence Index (Wagner, 1961) has been utilized. Characters have been assembled which can be valued 0.0 for primitive, 0.5 for intermediate, and 1.0 for derived. Designation of characters as primitive or derived is based on familiarity with the genus and generally accepted trends such as polyploidy or aneuploidy being derived characters and woodiness being a primitive character. The characters utilized are listed in Table 4. The divergence index values for the species are listed in Table 5. To conserve space, the characters are represented by their corresponding number in Table 4.

It must be understood that in a large genus such as *Tiquilia,* an overly complex set of values would be necessary for exact portrayal of inter-sectional and intra-sectional species relationships. To simplify matters, a few characters are weighted differently from section to section. For example, the character of open or closed nutlet scar: *T. hispidissima* of sect. *Eddya* is valued 0.0 as "open", while *T. ferreyrae* of sect. *Tiquilia,* with a wider scar, is valued 1.0 as "closed" in comparison with the other species in their respective sections. For purposes here, the base chromosome number for the genus is arbitrarily set at $x = 9$. When chromosome numbers are not known for a species, the number has been estimated, using exomorphic features as a primary guide.

Table 4. **Primitive and Derived Characters in Tiquilia.**

Primitive	Derived
1. Woody.	1. Herbaceous.
2. Leaves large and/or broad.	2. Leaves small and/or narrow.
3. Calyx not specialized.	3. Calyx indurated, plumose, or otherwise specialized.
4. Flowers in clusters.	4. Flowers solitary.
5. Corolla without appendages.	5. Corolla appendaged.
6. Stamens exserted.	6. Stamens included.
7. Style attachment apical.	7. Style attachment basal.
8. Nutlets 4 per fruit.	8. Nutlets consistently 2, or 1 per fruit.
9. Nutlets large, not spheroid.	9. Nutlets small, or spheroid.
10. Ornaments on nutlets small or absent.	10. Ornaments on nutlets large, or specialized extensions present on nutlet.
11. Nutlet scar broad.	11. Nutlet scar closed.
12. Diploidy.	12. Polyploidy.
13. Euploidy.	13. Aneuploidy.

Figure 5 is a diagram showing species relationships and degrees of advancement as calculated from the advancement index values in Table 5. The species are positioned according to their representative sections; the base of each line indicates the origin of the species it subtends.

It can be seen that the monotypic sect. *Stegnocarpus* has the most primitive characters. Because of this position, its flavonoid chromatograph pattern, unique for the genus, and its spheroidal fruit, which is approached only by species in sect. *Tiquilia*, *T. canescens* is judged to have diverged early in the history of the genus.

Sect. *Ptilocalyx*, another monotypic section, is judged to have diverged much later than sect. *Stegnocarpus*. Curiously, although inflorescence, fruit characters, and plant habit are unique in the subgenus, the leaves of *Tiquilia greggii* are essentially identical with those of *T. canescens* (sect. *Stegnocarpus*), and there is a strong similarity to those of *T. mexicana* (sect. *Eddya*). The globose inflorescence is interpreted as homologous with the inflorescence most common in subg. *Tiquilia*. *Tiquilia greggii* is the only species in subg. *Eddya* to demonstrate this affinity with subg. *Tiquilia*.

Table 5. **Divergence Index Values of the Species of Tiquilia.***

	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
T. canescens	0.5	0.5	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
T. greggii	0.0	0.5	1.0	0.0	1.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	4.5
T. latior	0.5	1.0	0.0	1.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5
T. hispidissima	0.5	1.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0	0.0	5.5
T. tuberculata	0.0	1.0	0.0	1.0	0.0	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	6.0
T. turneri	0.0	1.0	0.0	1.0	1.0	1.0	0.0	0.5	1.0	0.0	1.0	0.0	0.0	6.5
T. mexicana	1.0	0.5	0.0	0.5	0.5	1.0	0.0	0.5	1.0	1.0	1.0	0.0	0.0	7.0
T. gossypina	0.5	1.0	0.0	1.0	1.0	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	7.5
T. purpusii	1.0	0.5	0.0	0.5	0.5	1.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	6.5
T. nuttallii	0.5	0.5	0.0	0.0	1.0	1.0	0.5	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. plicata	0.5	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. palmeri	0.5	0.0	0.0	0.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	0.0	1.0	6.5
T. cuspidata	0.5	1.0	0.0	0.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	0.0	1.0	8.5
T. dichotoma	0.5	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	3.5
T. simulans	0.5	0.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	1.0	0.0	3.5
T. grandiflora	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0	1.0	0.0	3.5
T. ferreyrae	0.5	0.0	1.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	1.0	1.0	0.0	4.0
T. atacamensis	0.5	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	0.0	3.5
T. tacnensis	0.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	4.5
T. elongata	0.5	0.0	0.0	0.0	1.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	5.5
T. hunteri	0.0	1.0	0.0	0.0	1.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	1.0	7.0
T. litoralis	0.5	0.5	0.0	0.0	0.5	0.5	0.0	0.0	1.0	0.0	1.0	1.0	1.0	6.0
T. conspicua	0.5	0.0	0.0	0.0	1.0	0.5	1.0	0.0	1.0	0.0	1.0	1.0	0.0	6.0
T. paronychioides	0.5	1.0	0.0	0.0	0.0	1.0	0.5	0.0	1.0	0.0	1.0	1.0	0.0	6.0
T. nesiotica	0.5	1.0	1.0	0.5	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.0
T. galapagoa	0.5	1.0	1.0	0.5	0.0	1.0	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.0
T. darwinii	0.5	1.0	1.0	0.5	1.0	0.5	0.0	0.0	1.0	0.0	1.0	1.0	0.0	7.5

*Utilized characters are represented by numbers corresponding with the characters in Table 4.

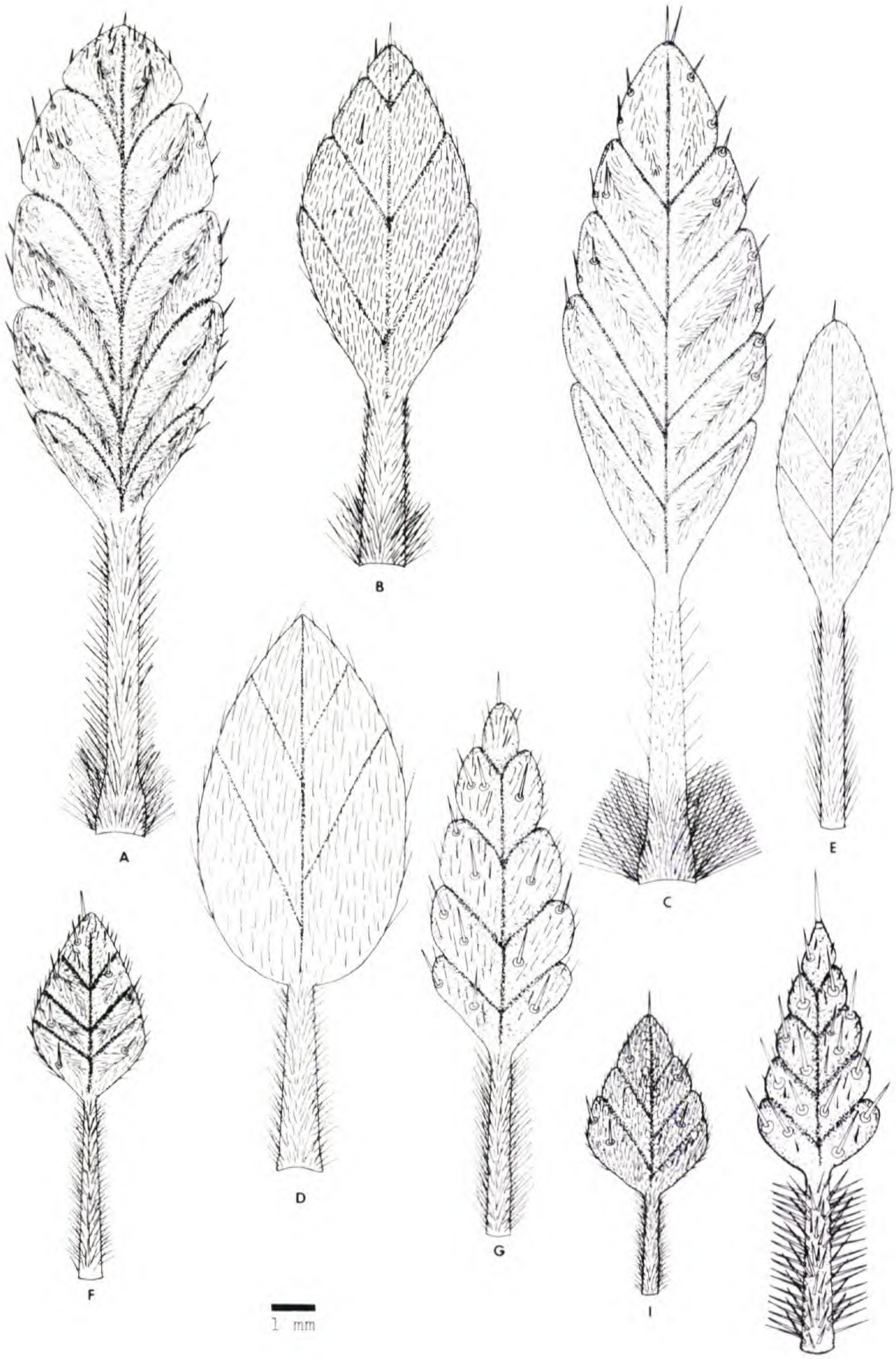

Figure 7. Drawings of leaves of *Tiquilia*. A, *T. dichotoma*; B, *T. simulans*; C, *T. grandiflora*; D, *T. ferreyrae*; E, *T. atacamensis*; F, *T. tacnensis*; G, *T. elongata*; H, *T. hunteri*; I, *T. litoralis*.

Sect. *Eddya* is dominated by a trend toward ovoid nutlets with a closed attachment scar and large ornaments. Fabre (1966) has noted a definite trend in the Boraginaceae for xeric plants to have rougher nutlets, and mesophytes to have smoother nutlets. There is also a trend toward a linear or lanceolate leaf blade, and generally reduced leaf size, the petiole often being extremely reduced and scale-like. *Tiquilia mexicana* follows this second trend only slightly, and *T. purpusii* not at all.

Tiquilia latior, the most primitive species of the section, has followed these general trends, but to a lesser degree than other species. Of special note is the obpyriform or rarely ovoid shaped nutlet with small ornaments and an attachment scar much narrower than in *T. greggii* but broader than those of any other species in its section. Also noteworthy is the geographic distribution of the species, viz. along the Colorado and Little Colorado River basins in Arizona, Nevada, and Utah, near the proposed center of origin of the genus (see below). The nutlets of the closely related species, *T. hispidissima,* have a slightly narrower attachment scar. This species grows farther east and south, in New Mexico, trans-Pecos Texas, and adjacent Mexico.

Tiquilia cuspidata of sect. *Tiquiliopsis* is the most derived species of the genus and is in a section containing well-advanced species. The section is characterized by a base chromosome number of $x = 8$; a trend from sub-apical to gynobasic style attachment; variety in nutlet shape; and innovations, such as the development of underground rhizomes (*T. plicata*), and loss of mericarps and resulting reduction of nutlets per fruit (*T. cuspidata*).

The tetraploids of sect. *Tiquilia* (where $n = 16$) seem to have an unusual concentration of primitive characters. This fact might possibly be attributed to polyploid buffering (Stebbins, 1971). Stebbins (1966) has noted that taxa with low chromosome numbers tend to undergo more differentiation than do taxa with high chromosome numbers.

The ovoid shaped fruit, usually of two nutlets, is of particular note in taxa of sect. *Tiquilia,* and the hemi-ovoid nutlets have broad, flattened, ventral surfaces. The pericarp covers only the convex surface, reminiscent of *Tiquilia canescens* of sect. *Stegnocarpus.* Since the pericarp character is lost in all North American species, excepting *T. canescens,* it is inferred that the movement of the ancestral stock into South America must have occurred at an

early point in the evolution of the genus. Doubling of the chromosome complement likely took place early in the development of the South American species, since there are no known diploids. A direct introduction of tetraploids from North America is possible, but no North American tetraploids have been found.

There is a definite trend toward inrolling of the pericarp. There is none in *Tiquilia dichotoma; T. simulans* has a slight inrolling; and *T. ferreyrae* has a more pronounced inrolling, the flattened ventral surface becoming correspondingly smaller. The stamens are consistently exserted in all species.

Sect. *Sphaerocarya* appears to be directly derived from advanced stock of sect. *Tiquilia*. Among the species of sect. *Sphaerocarya* there is a gradual shortening of the stamens from an exserted position to an intermediate and finally to an included position. There is also a continuation of the trend toward inrolling of the pericarp, and development of a spheroidal nutlet, culminating in *Tiquilia conspicua* with spheroidal nutlets and a gynobasic style; *T. litoralis* with spheroidal nutlets and reduction of chromosome number to $n = 15$; and *T. hunteri* with reduced spheroidal nutlets and chromosome number $n = 14$. Other species which have been counted are tetraploids, $n = 16$.

The species of sect. *Galapagoa* are characterized by ovoid, black nutlets, a loss of corolla color, and a reduction in size of all organs. Definite chromosome counts have not been obtained, but an approximate count (n = ca. 14–16) for *Tiquilia paronychioides*, the only mainland species, suggests polyploidy.

The relations of the species of sect. *Galapagoa* with other South American species are not clear, as indicated by a broken line in Figure 5. The nutlet characters are unlike those of any other species on that continent. Similarities between nutlets of *Tiquilia paronychioides* (sect. *Galapagoa*) and *T. cuspidata* (sect. *Tiquiliopsis*) suggest the possibility of a second introduction from North America. However, on the basis of morphological and chromosomal evidence it seems better to assume a closer relationship with the other South American sections and to attribute the similar nutlet characters to convergence in similar habitats. Additional chemical studies would provide useful evidence for determining these relationships.

Ancestral *Tiquilia* was presumably a member of the Madro-Tertiary Geoflora which, according to Axelrod (1958), apparently

was derived from the Neotropical Tertiary Geoflora. Johnson (1968) includes *Coldenia* (sensu lato) with plants showing relationships with southern and western elements rather than with northern elements. Rzedowski's (1973) conclusions also support the hypothesis of a Neotropical origin of *Tiquilia*. The subfam. Ehretioideae is, of course, typically of tropical or warm temperate affinities.

It is impossible to fix accurately the time and place of origin of *Tiquilia*. There is no fossil record. However, the history of the genus probably began in western North America. The trend toward aridity beginning in Eocene and Oligocene times gave a selective advantage to, and allowed the spread of, semi-xeric plants previously limited to scattered xeric pockets. The generally xeric conditions of the succeeding Miocene time probably favored the establishment and radiation of *Tiquilia*.

The two subgenera, after or concomitant with spatial separation, were further separated by differences in chromosome numbers and ecological adaptations. The divergence occurred at an early point in the evolution of the genus, as evidenced by the primitive morphological characters, previously discussed, in the South American sect. *Tiquilia*.

Subg. *Eddya* ($x = 9$), developing a tolerance for infertile gypseous soils, was able to move into the relatively open habitats in gypseous areas toward the east, particularly in New Mexico and eastward and southward into Texas and Mexico. Speciation was enhanced by edaphic conditions, with fertile soils interrupting gypseous areas and providing effective barriers between populations that might otherwise be continuous (see Grant, 1963, p. 456; 1971, p. 114). Continuing orogeny in the late Pliocene and Pleistocene times brought more extreme xeric conditions and inhibited further migration.

Subg. *Tiquilia* ($x = 8$) was limited to the western part of the continent, migration being mostly northward and southward. Edaphic adaptations were toward "pure" sand, or sandy soils. Sect. *Tiquiliopsis* was established in western North America. The four extant species are well differentiated and distinct.

A segment of the stock moved into South America, possibly by long-distance dispersal, or by a series of shorter steps along dry coastal pockets. Speciation was probably enhanced by topography and edaphic conditions, with frequent habitat interruptions by

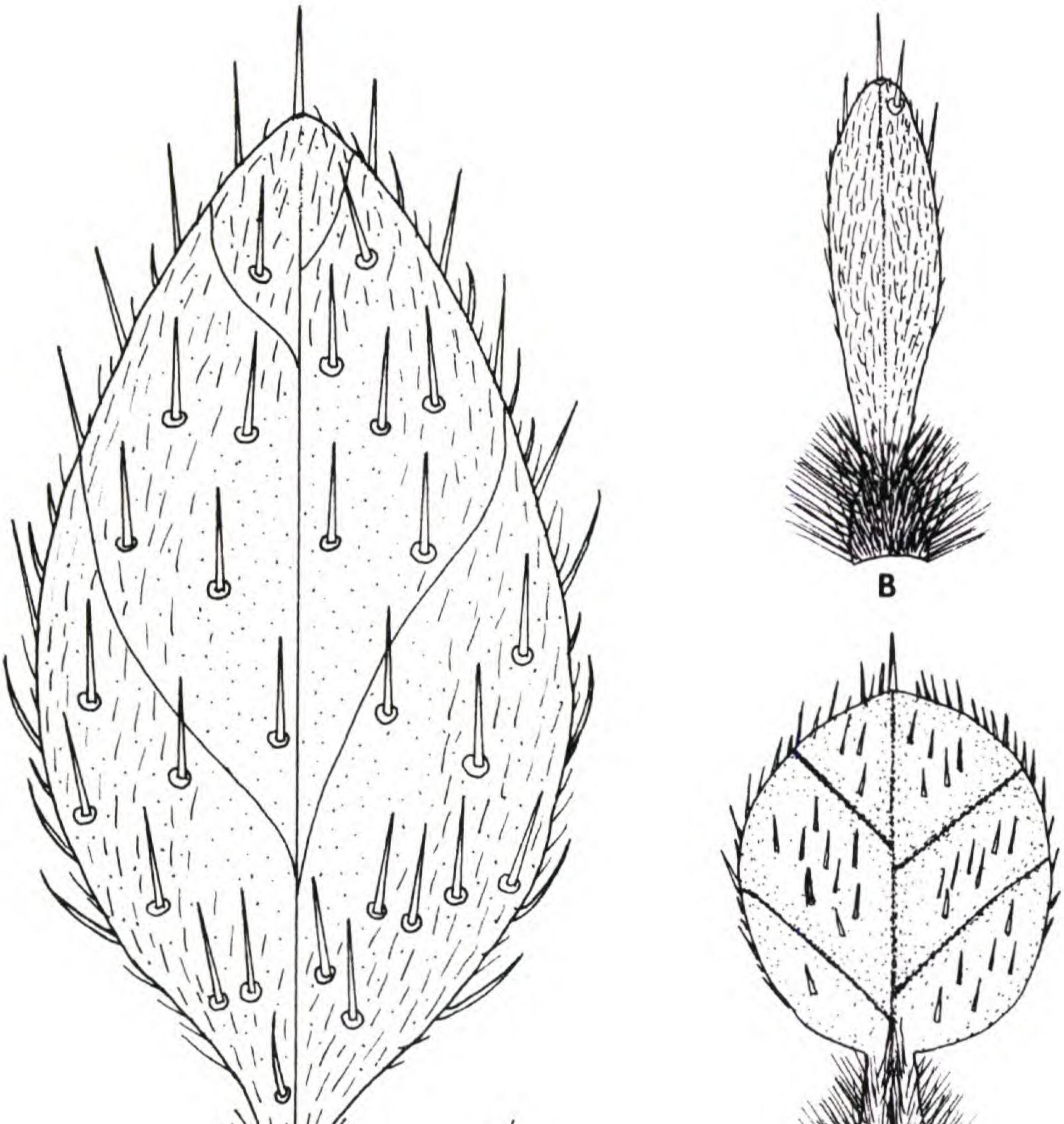

Figure 8. Drawings of leaves of *Tiquilia*. A, *T. conspicua;* B, *T. paronychioides;* C, *T. galapagoa;* D, *T. nesiotica;* E, *T. darwinii.*

mountains and fertile river valleys. The center of variation is southern Peru.

DISPERSAL OF DISJUNCT TAXA

The subject of amphitropical disjuncts has been discussed by Bray (1900), Johnston (1940), and others (Constance, 1963; Grant, 1959; Heckard, 1963; Raven, 1963), and more recently by Hunziker (1972), Raven (1972, 1974), Turner (1972), and Werger (1973). Hunziker *et al.* (1972) interpreted their data on *Larrea* as indicating a South American origin of the genus and a later introduction into North America. However, Turner (1972) and Porter (1974) visualized the reverse as equally possible. Sanderson (1975) used chemical, morphological, and cytological data to show that North American *Hymenoxys odorata* and *H. anthemoides* were not as closely related as their morphology seemed to suggest. Following Turner (1972), he classified them as allojuncts. Payne *et al.* (1973), using sesquiterpene lactone chemistry, found that the North American and Chilean populations of *Ambrosia chamissonis* represent one variable species presumably derived from extant North American populations; accordingly, they are autojuncts (Turner, 1972).

Cytological and morphological data indicate that all the South American species of *Tiquilia* in sects. *Tiquilia, Sphaerocarya,* and *Galapagoa,* being derived from extinct North American stock, are allojuncts. However, populations of *T. nuttallii* (sect. *Tiquiliopsis*), occurring in the northwestern United States and northwestern Argentina have apparently identical morphology and flavonoid chromatograph patterns. Unfortunately, chromosome counts have not been obtained from any South American populations of this species. In the absence of conflicting data, the South American populations of *T. nuttallii* are considered autojuncts.

Three explanations have been offered for the presence of transtropical disjunct, closely related taxa on the two continents: (1) an old American desert was shared, and continuous with both continents, (2) migration took place by a series of steps through isolated hospitable habitats, or (3) by one or few long jumps (long distance dispersal).

The first explanation has been rejected for the following reasons: (1) there was no continuous land connection between North Amer-

ica and South America until about the Pliocene (Raven & Axelrod, 1974); (2) relatively few plants, and no vertebrates, have been exchanged (Raven, 1963); (3) the tropical forest has always occupied the central area within the tropics (Grant, 1959); and (4) fossil evidence indicates that floras of North and South America were separated and developed independently during Paleozoic and Mesozoic times (Constance, 1963).

The remaining two explanations seem highly unlikely; however, the plants are there and they must have arrived by one of these methods. As stated by Grant (1959), the two methods are not mutually exclusive.

Although desert vegetation did not reach its present aspect until Pliocene time (Johnson, 1968), desert areas were probably present at least by Miocene time (Turner, 1972). Although there was no continuous Central American land bridge, recent opinions are that throughout Tertiary time there were shifting groups of islands and peninsulas attached at different times to one continent or the other (Bartlett & Barghoorn, 1973). This unstable condition would no doubt present a series of open habitats by which *Tiquilia* could have crossed to the South American mainland. The large primitive fruit was probably buoyant (as is that of *T. canescens*) and could have been transferred from island to island by drift, rafting, or by birds. *Tiquilia* in Central America could have been eliminated after subsequent stabilization of the land and introduction of more competitive plants.

The feasibility of long-distance dispersal by birds has been discussed with both negative and affirmative opinions. Cruden (1966) discarded the possibility of external transport because propagules would be unlikely to remain attached after repeated preenings and exposure to the elements during the time (one month) that he estimated would be required for the trip. He believed internal transport was impossible because seed passage takes only a few hours. He further questioned whether the amount of genetic variability transported in one or a few seeds would be sufficient to account for the morphological variation exhibited by various taxa.

Carlquist (1967, 1974), on the other hand, believes many introductions to remote islands were made by birds. Grant (1959) affirmed the plausibility of birds as vectors of long-distance dispersal between North and South America. He noted that all of the twelve herbaceous species of the Polemoniaceae in South America have

mucilaginous seeds, although, in some cases, this feature represents an exceptional condition for the genus or section.

Tiquilia has no adaptations for long-distance dispersal on the external anatomy of birds, and there is no indication that the ancestral stock had any. The taxa occur in sandy rather than muddy habitats, and their fruits are not mucilaginous or spiny. The closely related *Coldenia procumbens* sometimes produces fruits with some spinelike processes; however, the processes are broad and blunt and, in the opinion of this investigator, would not cause the fruits to adhere to a bird.

The remaining possibility is internal transport. *Tiquilia* fruits are inconspicuous and dry and therefore do not seem particularly adapted for dispersal by birds. However, many of the migratory shore birds eat various types of plant material. *If* the nutlets could remain in the bird's gut, undamaged, until arrival at a suitable habitat, then there is reason to consider the possibility of birds as agents of long-distance dispersal of *Tiquilia.*

The calculated age of the Galapagos Islands, about one million years, limits the time of migration to the islands and subsequent evolution of the three Galapagoan species to the same time period. Nutlets were transported from the South American mainland to the islands possibly by oceanic drift, rafting, or by birds. Carlquist (1967), in analyzing the flora of the Galapagos Islands, believed many introductions were made by oceanic drift as well as by birds. The nutlets of the species in this section do not float, but could have been transported with portions of the plant or on other buoyant material. Previous adaptation to dry, sandy habitats would facilitate establishment on a beach and subsequent inter-island dispersal, once the islands were reached. However, it is not known whether the seeds would survive long periods of immersion in salt water.

There being no spines or viscid material on the nutlets, they would have to be carried internally if birds are the vectors. There are, however, no data concerning feeding habits of birds on *Tiquilia.*

TAXONOMIC TREATMENT

Tiquilia Persoon, Syn. Pl. **1:** 157. 1805.

Monomesia Raf., Flora Telluriana **4:** 87. 1836, *nomen. superfl.*, based on an unnamed specimen collected by Dombey (*Dombey 364*), probable duplicate GH!), described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible con-

gener of *Coldenia*.
Galapagoa Hook. f., Trans. Linn. Soc. **20:** 196, 197. 1847.
Stegnocarpus Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 169. *Pl. 7.* 1857.
Eddya Torrey & Gray, *Ibid.:* 170. *Pl. 9.* 1857.
Ptilocalyx Torrey & Gray, *Ibid.:* 170. *Pl. 8.* 1857.

Pseudo-dichotomously branching perennials often flowering the first year, fruticose or suffrutescent (bark, when present, usually exfoliating) or herbaceous, prostrate, spreading or bushy-branched; pubescence variable. Leaves solitary at the nodes or in clusters on short branches, stem apices, or the nodes; blades green to grey, linear to lanceolate, ovate, obovate, or suborbicular, 2.5–23.0 mm. long, margins revolute, entire or crenate, the lateral veins running to the sinuses when crenate; petioles subrectangular to ovate-trullate or filiform, or a combination of both. Flowers sessile, solitary or few and axillary, or in clusters usually subtended by bracts. Calyces 5-lobed, the lobes triangular to lanceolate, narrowly ovate, or subulate. Corollas white to pale lavender to deep blue or purple, often with a yellow throat; deciduous in North America, deciduous or persistent in South America, funnelform, occasionally cylindrical; lobes 5, rounded, imbricate in bud. Stamens 5, included in North America, included or exserted in South America, equal or unequal, adnate to the corolla tubes usually at 3 levels, sometimes equally, level of insertion variable. Styles cleft once, the stigmas capitate; attachment to nutlets apical, sub-apical, sub-basal, or basal. Nutlets 1–4. Cotyledons (after germination) elliptic or hippocrepiform. Base chromosome numbers, $x = 9$, $x = 8$; derived chromosome numbers, $n = 16$, 15, 14. TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

The name for the genus was taken from the vernacular name of the type species, *Tiquil-tiquil.* The vernacular name is probably a derivative of the Quechua word *t'ika,* meaning flower.

Tiquilia consists of two subgenera. One subgenus comprises three sections, and the other, four. The subgenera and the sections can be distinguished by the following key.

KEY TO THE SUBGENERA & SECTIONS OF TIQUILIA

a. Nutlet ovoid to obpyriform, with collicula or tubercula 0.05 mm. across or larger; or if ornaments are smaller or absent, the nutlets 0.8 mm. or longer, and the petiole elliptic-rectangular, or the nutlet pubescent apically, or the fruit

spheroid, of 4 nutlets. Style attachment apical. North America: United States and Mexico. ..... 1. *Tiquilia* subg. *Eddya* (page 505, species 1–9).
b. Fruit lobed, not spheroid. ..... c.
c. Plant procumbent, herbaceous from a woody caudex or if shrubby, not erect; nutlet not pubescent, not retained in a plumose calyx. ..... 1c. *Tiquilia* sect. *Eddya* (page 514, species 3–9).
c. Plant an erect shrub, fruit of 1 nutlet, pubescent apically, retained in a plumose calyx. ..... 1b. *Tiquilia* sect. *Ptilocalyx* (page 510, species 2).
b. Fruit not lobed, spheroid, of 4 nutlets. ..... 1a. *Tiquilia* sect. *Stegnocarpus* (page 506, species 1).
a. Nutlet ovoid to spheroid, minutely colliculate, minutely aculeate, granular (in all cases, the ornaments smaller than 0.04 mm. across), or smooth. Style attachment apical, sub-apical, sub-basal, or basal. North and South America. ..... 2. *Tiquilia* subg. *Tiquilia* (page 530).
d. Nutlet not hemi-ovoid, ventral surface not broadly flattened; corolla deciduous; stamens included or slightly exserted. ..... e.
e. Nutlet ovoid, without the corresponding characters of sect. *Sphaerocarya;* or spheroid, smooth or minutely aculeate with a gynobasic style. ..... f.
f. Nutlet ovoid, the attachment scar running almost the full length, terminating more or less equidistant from apex and base; style attachment apical or sub-apical; petiole ovate-trullate. South America. ..... 2d. *Tiquilia* sect. *Galapagoa* (page 560, species 24–27).
f. Nutlet spheroid or ovoid; style attachment sub-apical, sub-basal, or basal; petiole filiform, or if trullate then the nutlet attachment scar beginning near the base running more or less ¾ the length, and style attachment basal. North and South America. ..... 2a. *Tiquilia* sect. *Tiquiliopsis* (page 530, species 10–13).
e. Nutlet spheroid (exclude if style is gynobasic and nutlets are without a basal plug and either smooth or minutely aculeate), or ovoid in ventral view, elliptical and beaked in lateral view, mottled grey, brown, and black. South America. . 2c. *Tiquilia* sect. *Sphaerocarya* (page 550, species 18–23).
d. Nutlet hemi-ovoid, ventral surface broadly flattened, corolla persistent, stamens greatly exserted, 3.0–8.0 mm. South America. ..... 2b. *Tiquilia* sect. *Tiquilia* (page 542, species 14–17).

Tiquilia subg. **Eddya** A. Richardson. TYPE SPECIES: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Leaf margins entire. Nutlets ovate to obpyriform, with colliculа or tubercula 0.05 mm. across or larger; or if ornaments are smaller or absent, the nutlets 0.8 mm. or longer, and the petioles elliptical-rectangular, or the nutlets pubescent apically, or the fruit spheroid, of 4 nutlets. Stamens unequal, included, adnate to the corolla tubes at 3 levels. Style attachments apical. Cotyledons (after germination) elliptical. Chromosome number, $n = 9$ (one species aneuploid with $n = 8$).

Tiquilia sect. **Stegnocarpus** DC., Prodr. Syst. Nat. **9:** 559. 1845.

TYPE SPECIES: *Tiquilia canescens* (DC.) A. Richardson.

Herbaceous to suffrutescent. Leaves solitary at the nodes and in clusters on short branches or the stem apices; blades ovate, lanceolate, or obovate. Flowers axillary, solitary, occasionally 2 or 3. Calyces persistent. Fruits spheroidal. Chromosome number, $n = 9$.

The single species in this section is the most widespread of the genus, found in the United States and Mexico from the Texas gulf coast to the Pacific coast.

1. **Tiquilia canescens** (DC.) A. Richardson, Sida **6:** 236. 1976. Synonymy and typification are cited under the varietal headings. Herbaceous to suffrutescent, procumbent or spreading, 1.0–3.0 dm. high, with one report of a shrub to 6.0 dm. high, forming mounds or mats to 6.0 dm. across from woody taproots; caudices to 2.0 cm. thick; younger branches villous with some thin stiff spreading hairs to 0.9 mm. long; short branches often appearing on alternating sides of the main stem, giving a zigzag effect. Leaves solitary, axillary, or in clusters on short branches; blades (Figure 6A) green to grey or nearly white, 7.0–11.5 mm. long, 4.0–8.5 mm. broad, ovate, lanceolate, or obovate, sometimes decurrent on the petiole, curling back markedly under dry conditions, otherwise fairly flat except for a tendency in western United States and Mexico for the leaves to roll slightly, giving convex upper surfaces, the blades appearing thicker; upper surfaces densely pubescent with short straight variously appressed hairs, overlaid with antrorsely appressed or inclined larger stiff bristles to 0.6 mm. long with thickened mineralized bases, these sometimes more prominent along the margins; lower surfaces more densely pubescent; petioles filiform, 1.5–7.0 mm. long, villous with dense spreading bristles to 0.9 mm. long. Calyces persistent, 3.0–5.0 mm. long, villous and densely covered by fine straight antrorsely inclined or appressed hairs to 0.9 mm. long on outer surfaces; lobes subulate, linear or triangular, slightly unequal, sometimes ciliate, with sparse antrorsely appressed hairs on inner surfaces, free 2/3 to 3/4 the length. Corollas opening in the morning and falling in the evening; white to pink, purple, or blue, often with a yellow throat, 3.5–9.0 mm. long, not appendaged; the bud glabrous or villulose. Stamens adnate to the corolla tubes ca. 1/4 the length from base to limb. Styles 2.0–3.5 mm. long, cleft 1/3 the

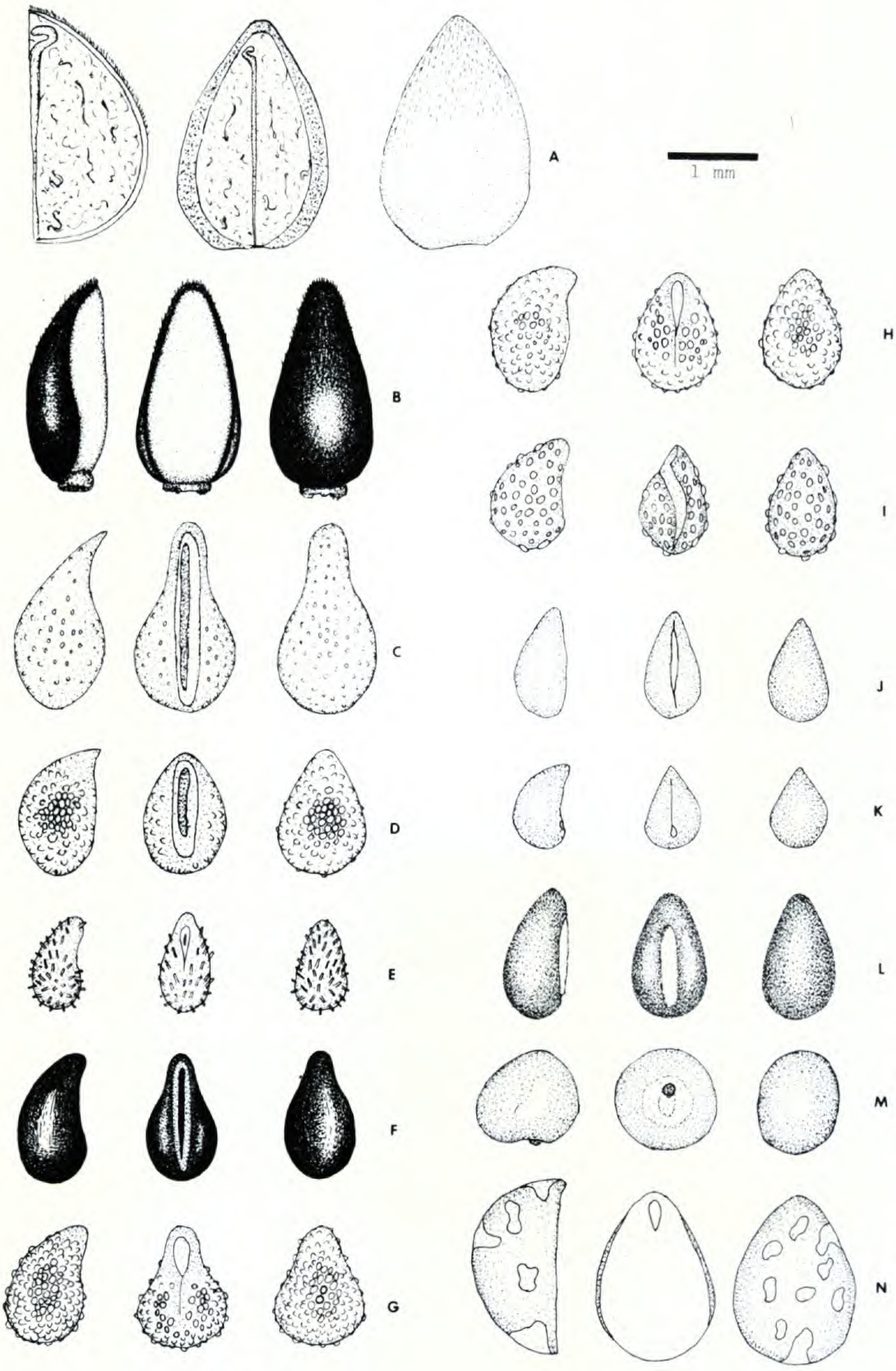

Figure 9. Drawings of nutlets of *Tiquilia,* left to right, lateral, ventral, and dorsal views. A, *T. canescens;* B, *T. greggii;* C, *T. latior;* D, *T. hispidissima;* E, *T. tuberculata;* F, *T. turneri;* G, *T. mexicana;* H, *T. gossypina;* I, *T. purpusii;* J, *T. nuttallii;* K, *T. plicata;* L, *T. cuspidata;* M, *T. palmeri;* N, *T. dichotoma.*

length, occasionally less; stigmas large, subbifurcate. Fruits spheroidal with 4 longitudinal grooves, 2.1–3.0 mm. across, 2.2–2.8 mm. high, exocarp thickened, smooth or minutely colliculate, shiny light brown to dull dark brown, glabrous or puberulent apically, sometimes over all with short, retrorsely appressed straight hairs; nutlets (Figure 9A) 1–4, usually 4.

Tiquilia canescens is often the dominant plant where it grows, but it also grows with such dominants as *T. greggii, T. hispidissima, Gutierrezia microcephala, Larrea, Leucophyllum, Pinus,* and *Yucca.* It also grows in association with *Acacia, Agave, Dasylirion, Fouquieria, Franseria, Prosopis, Nerisyrenia, Opuntia, Selinocarpus,* annuals, and grasses. It has been observed *in situ* with five other species of *Tiquilia: T. gossypina, T. greggii, T. hispidissima, T. mexicana,* and *T. purpusii,* and is geographically sympatric with *T. cuspidata, T. nuttallii, T. palmeri,* and *T. plicata.*

Two varieties are recognized. Their distributions are shown in Figure 11. They may be distinguished and characterized by the following key.

KEY TO THE VARIETIES OF TIQUILIA CANESCENS

Corolla 3.5–7.5 mm. long. ..... 1a. *T. canescens* var. *canescens.*
Corolla 7.0–9.0 mm. long. ..... 1b. *T. canescens* var. *pulchella.*

1a. **Tiquilia canescens** var. **canescens**

Coldenia canescens DC., Prodr. Syst. Nat. **9:** 559. 1845. TYPE: **Mexico:** Tamaulipas. Inter Santander (Jimenez) et Victoria, *Berlandier 2256.* (Holotype, G, not seen. Photograph TEX! Isotypes, GH! NY! US! Possible isotype, NY!).

Stegnocarpus canescens (DC.) Torr., *In* Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 169–170. *Pl. 7.* 1857.

Coldenia canescens var. *subnuda* I. M. Johnst., Proc. Calif. Acad. IV. **12:** 1137. 1924. TYPE: **Mexico:** BAJA CALIFORNIA. San Nicolas Bay, 16 May 1921, *I. M. Johnston 3731.* (Holotype, CAS! Isotypes, F! GH! NY! UC! US!).

DISTRIBUTION: *Tiquilia canescens* var. *canescens, n* = 9, is by far the most widespread taxon of the genus. It grows in Arizona; southeastern California; southern Nevada; southern New Mexico; in Texas from El Paso County eastward to Bexar County and from Kent County southward to Cameron County; in Mexico in Baja California; eastern Chihuahua; Coahuila; northwestern Hidalgo; Nuevo Leon; Querétaro; San Luis Potosí; Sonora; Tamaulipas; and eastern Zacatecas (Figure 11). It grows from the xeric extremes of

Baja California and the southeastern California deserts to the moderately xeric conditions of south Texas; from the moderate temperature ranges in the Mexican states of Hidalgo and Querétaro, well south of the Tropic of Cancer, to the harsher extremes of southern Nevada; at altitudes from 8 meters to 2530 meters; in gypseous or calcareous loam or clay, or in desert sands. It is the only North American taxon showing any consistent ability to compete with other plants, often growing with grasses and annuals, although more often growing in the absence of any competition.

As with the other taxa, flowering is controlled by moisture availability, the plants becoming dormant and dying back during extended dry periods. The plants flower January through December in Texas, but less in other localities.

Vernacular names are Oreja del Perro and Yerba del Pobre. In Mexico, a decoction of leaves and stems is used to bathe wounds (*Latorre 15* TEX). It is also used for sweat baths, and to prevent going to sleep after eating (*Lundell 5266* LL). Conflicting data on herbarium labels report no forage value (*JTC-Kav s.n.* GH), and good forage value (*Hershey 3415* GH). Personal observations in various conditions including areas where cattle and goats were grazing, indicate there is little or no forage value, since no grazing damage to plants has ever been seen. The only plant part damaged by insects is the corolla.

Johnston (1924) first differentiated *Coldenia canescens* var. *subnuda* on the basis of fruit pubescence. Later (1966) he found this character inconsistent, but he retained the variety on the basis of leaf size, color, and pubescence. There is no geographical correlation of those characters to justify a varietal status; rather there is a scattering throughout the distribution range, with plants having characters of the two "varieties" often in the same population.

1b. **Tiquilia canescens** var. **pulchella** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia canescens var. *pulchella* I. M. Johnston, Jour. Arnold Arb. **20:** 379. 1939. TYPE: **Arizona:** YUMA CO. Kofa Mountains, 1700 ft., 24 Mar. 1933, *Shreve 6527.* (Holotype, GH! Isotypes, ARIZ! F!).

DISTRIBUTION: This variety is known only in extreme southwestern Arizona (Yuma Co., rarely Yavapai Co.), and southeastern California (Imperial Co., rarely Riverside Co.) in association

with *Fouquieria, Franseria, Larrea,* and *Parkinsonia.* It is almost completely isolated geographically from *Tiquilia canescens* var. *canescens* (Figure 11).

Johnston (1939) described *Coldenia canescens* var. *pulchella* based on geographic correlation of greater corolla length and limb diameter, and intense corolla color. In this investigation, the corollas were found to be somewhat smaller than reported by Johnston. He probably soaked them prior to measuring them since, upon wetting, they increase in length about the difference between his measurements and those of this investigator. It seems more practical and useful to use measurements of dried corollas. Herbarium label data show corolla color comparable to that of *T. canescens* var. *canescens.*

This variety flowers February through June; September, November, and December.

No chromosome counts have been reported.

Tiquilia sect. **Ptilocalyx** A. Richardson. TYPE SPECIES: *Tiquilia greggii* (Torrey & Gray) A. Richardson.

Erect shrubs to 1.0 meter tall. Leaves in axillary or terminal clusters. Flowers in terminal bracteate globose clusters. Calyces plumose, deciduous, retaining the fruits. Fruits single nutlets, 3 mericaps aborting, remaining on the ventral surfaces of the nutlets as a membranous tissue. Nutlets ovoid-obpyriform, apically puberulent with spreading and retrorsely appressed hairs. Chromosome number $n = 9$.

This monotypic section includes a species found in northern Mexico, southern New Mexico, and trans-Pecos Texas.

2. **Tiquilia greggii** (Torrey & Gray) A. Richardson, Sida **6:** 236. 1976.

Ptilocalyx greggii Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 170, 171. *Pl. 9.* 1857. TYPE: Common in New Mexico, May-October 1849, *Wright 492* (Holotype, GH! Isotypes, GH! NY! UC! US!).

Coldenia greggii (Torrey & Gray) Gray, Proc. Am. Acad. **5:** 340, 341. 1862.

Low erect shrubs to 1.0 meter tall, compact, branches numerous and crowded; base to 1.3 cm. diameter; young branches villous with occasional stiff bristles to 0.7 mm. long. Leaves (Figure 6B) cinereous, sometimes greenish; blades ovate or elliptic, 4.5–8.5 mm. long, 2.1–4.2 mm. broad; upper surfaces covered densely with short

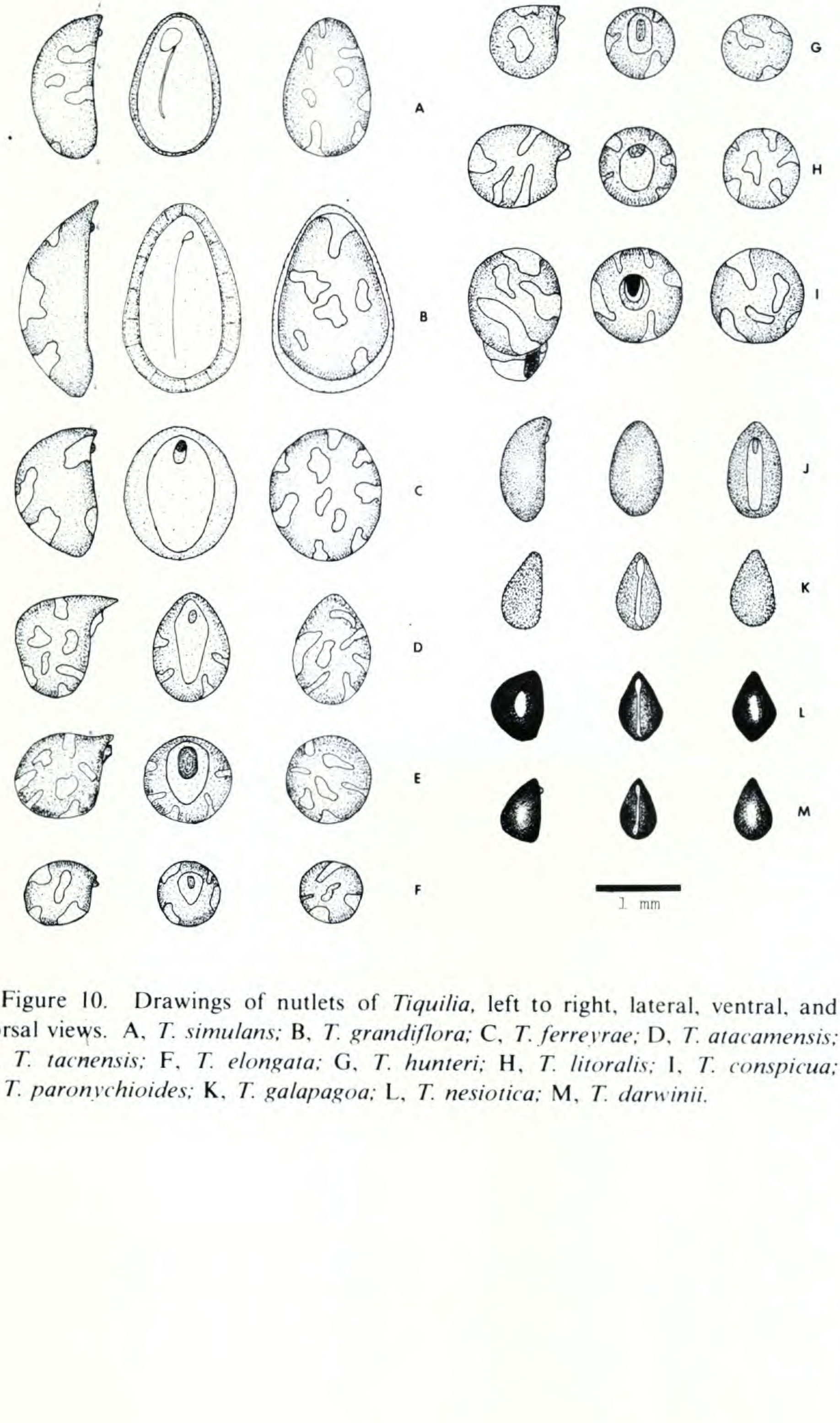

Figure 10. Drawings of nutlets of *Tiquilia,* left to right, lateral, ventral, and dorsal views. A, *T. simulans;* B, *T. grandiflora;* C, *T. ferreyrae;* D, *T. atacamensis;* E, *T. tacnensis;* F, *T. elongata;* G, *T. hunteri;* H, *T. litoralis;* I, *T. conspicua;* J, *T. paronychioides;* K, *T. galapagoa;* L, *T. nesiotica;* M, *T. darwinii.*

straight hairs appressed at various angles, these overlaid with antrorsely appressed or sharply inclined larger stiff bristles to 0.7 mm. long with thickened mineralized bases; lower surfaces somewhat more densely pubescent; petioles filiform, 0.5–1.5 mm. long with spreading hairs to 0.5 mm. long. Inflorescences terminal compact bracteate cymes, flowers appearing in conspicuous globose clusters 1.0–2.0 cm. across, the bracts linear to filiform, often resembling the calyx lobes. Calyces deciduous, enclosing the fruits, 5.0–7.5 mm. long, plumose with spreading thin stiff bristles to 1.3 mm. long on outer surfaces and upper half of inner surfaces; lobes unequal, free 4/5 the length, lanceolate, the apices filiform. Corollas opening in the morning and falling in the evening, pink to purple, 5.0–7.7 mm. long; villulose on outer surface near margin; the buds villulose. Stamens adnate to the corolla tube ca. 1/5 the length from base to limb, the veins below the points of attachment winged. Styles 2.1–3.3 mm. long, cleft 1/7–1/4 the length. Fruits (Figure 9B) single nutlets, ovoid-obpyriform, 1.8–2.5 mm. long, 0.9–1.2 mm. across, with tiny hairs spreading at the apex, retrorsely appressed and becoming more sparse below the apex to about the middle; exocarp thin, not indurated, dorsal surfaces purplish-black and shiny, ventral surfaces brown with a membranous tissue formed from 3 aborted mericarps. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia greggii* is found in xeric regions of southern New Mexico and trans-Pecos Texas, and in Mexico in eastern Chihuahua; Coahuila; northeastern Durango; eastern Nuevo Leon; northern San Luis Potosí; and northern Zacatecas (Figure 12). It grows on hilltops or slopes or desert flats in gypseous or limestone, often rocky soils with *Euphorbia antisyphilitica, Fouquieria splendens,* and species of *Agave, Larrea, Leucophyllum, Nerisyrenia, Prosopis,* and *Yucca,* and various cacti and grasses. It is often the dominant plant and usually does not grow in close proximity with other plants. It grows with four other species of *Tiquilia: T. canescens, T. gossypina, T. hispidissima,* and *T. mexicana,* and is geographically sympatric with *T. purpusii* and *T. turneri.*

Flowering season is April to November, whenever there is enough moisture.

In Mexico, it is called Yerba de la Cachucha and Regeneradora, and is used medicinally to treat gonorrhea (*Kelly 829,* UC).

Tiquilia greggii differs from all other *Tiquilia* species in (1) its

erect, shrubby habit. *Tiquilia turneri* and *T. tuberculata* are woody subshrubs, but not erect. The same is true of other taxa which are sometimes woody. (2) Reduction of nutlets to one by abortion of 3 ovules. (3) Adaptation for wind dispersal of the seed from a terminal inflorescence by retention of a single nutlet in a plumose calyx which falls when mature. The leaves resemble those of *T. canescens* and *T. mexicana,* while the inflorescence resembles that of the species of western North America and South America. *Tiquilia greggii* shows no close affinity to any other species of *Tiquilia* and can be easily identified at a glance.

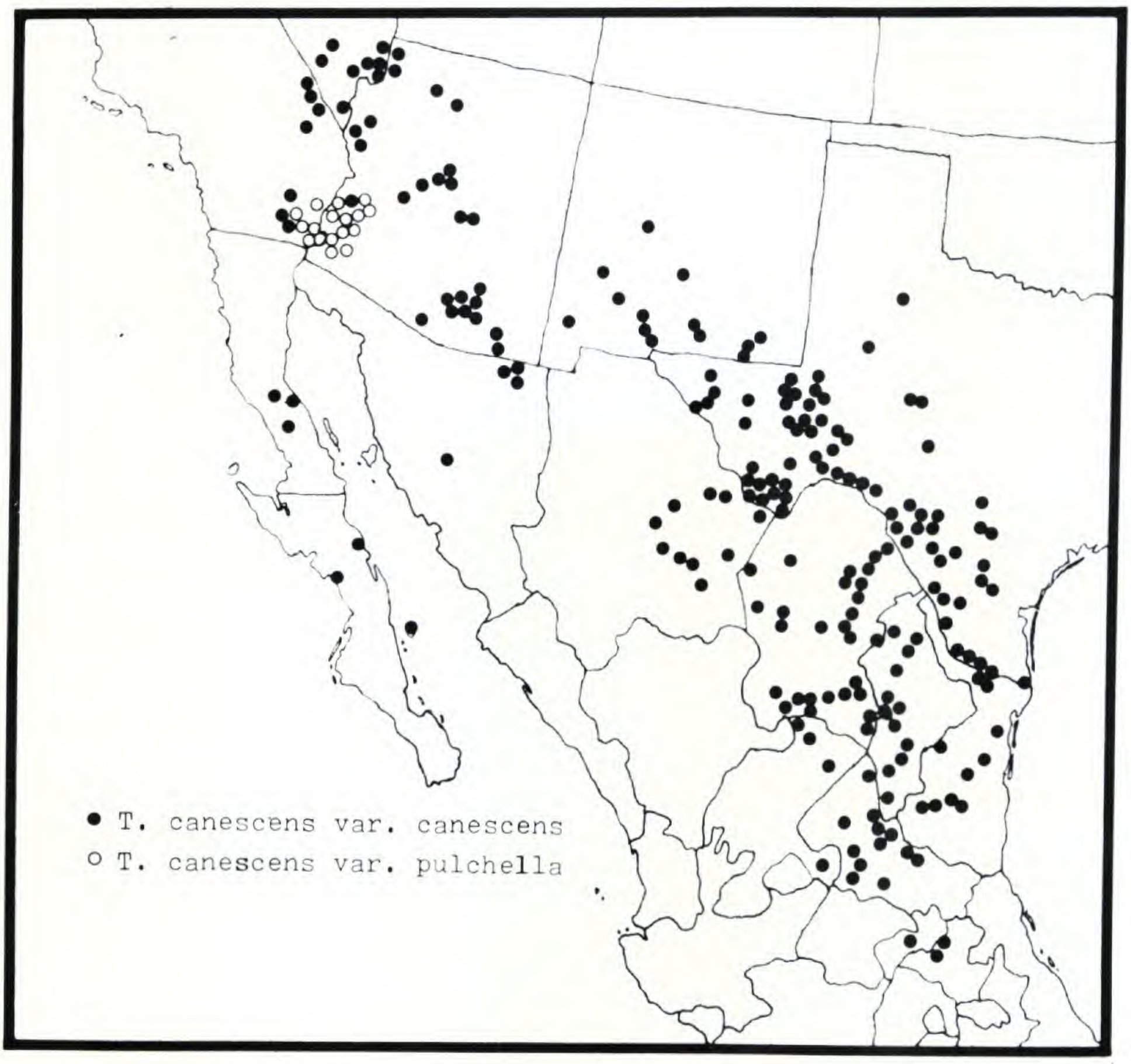

Figure 11. Distribution of *Tiquilia canescens* var. *canescens* and *T. canescens* var. *pulchella.*

Torrey and Gray (1857) chose the generic name *Ptilocalyx* from the Greek *Ptilo,* meaning down, feather, or wing, referring to the plumose calyx. This appropriately descriptive epithet is retained as the sectional name.

1c. **Tiquilia** sect. **Eddya** Gray, Proc. Am. Acad. **5:** 340. 1862.

TYPE SPECIES: *Tiquilia hispidissima* (Torrey & Gray) A. Richardson.

Procumbent or spreading, herbaceous, suffrutescent or fruticose. Leaves solitary at the nodes and in clusters on short branches or the stem apices; blades linear, oblong, narrowly ovate-obovate and needle-like, or ovate, bristly. Flowers solitary, axillary, or in small clusters with the leaves. Calyces persistent. Fruits lobed, of 1–4 nutlets; nutlets ovoid or obpyriform, somewhat indurated and colliculate or tuberculate, or smooth, not indurated. Chromosome number, $n = 9$ (*Tiquilia purpusii* with aneuploids, $n = 8$).

This is the most widespread section, including seven species of North America.

KEY TO THE SPECIES OF TIQUILIA SECT. EDDYA

a. Leaf blade length three times the width or more, petiole short, elliptic-rectangular. ..... b.
  b. Nutlet attachment scar narrow (0.2 mm. or less), open only above the middle or tapering to a point near the base; the bud glabrous or glandular. .... c.
    c. Nutlet white-colliculate, granular, or smooth; corolla winged below stamen attachments, the bud glandular or glabrous. ..... d.
      d. Nutlet black, smooth or granular, not indurated. ..... 6. *T. turneri.*
      d. Nutlet black, white-colliculate, indurated. ..... 8. *T. gossypina.*
    c. Nutlet white-tuberculate; corolla not winged below stamen attachments, the bud glandular. ..... 5. *T. tuberculata.*
  b. Nutlet attachment scar broad (0.3–0.5 mm.), open well below the middle; the bud villulose. ..... e.
    e. Leaf 5.0–17.0 mm. long, 1.1–4.2 mm. broad, blade obovate to narrowly obovate, petiole densely ciliate; nutlet obpyriform to ovoid, 1.5–2.0 mm. long, with white or brown collicula 0.04 mm. across or less. . 3. *T. latior.*
    e. Leaf 4.0–8.0 mm. long, 0.5–2.0 mm. broad, blade linear to narrowly obovate, petiole not noticeably ciliate; nutlet ovoid, 1.0–1.5 mm. long, with white collicula 0.05 mm. across or more. ..... 4. *T. hispidissima.*
a. Leaf blade length twice the width or less, petiole filiform at least in part. ..... f.
  f. Nutlet dark brown or black, the attachment scar and suture running straight from apex to base; leaf blade usually cinereous, upper surface with two kinds of hairs. ..... 7. *T. mexicana.*

f. Nutlet greenish or slate color, the attachment scar and suture running obliquely from apex to base; leaf blade usually green, upper surface with one kind of hair. ..... 9. *T. purpusii.*

3. **Tiquilia latior** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia hispidissima (Torrey & Gray) Gray, var. *latior* I. M. Johnston, Contr. Gray Herb. **68:** 92. 1923. TYPE: **Nevada:** CLARK CO.[2] Muddy Valley, 1700 ft., 16 May 1906, *Kennedy & Goodding 79.* (Holotype, GH! Isotypes, ARIZ! F! UC! US!).

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 5.0 dm. broad from a woody taproot; caudices to 1.0 cm. thick; branches villous with large pungent spreading bristles to 1.9 mm. long with thickened mineralized bases. Leaves (Figure 6C) in clusters on short, brittle branches, 5.0–17.0 mm. long, 1.1–4.2 mm. broad; blades obovate, occasionally linear; upper surfaces bright green and prickly with large bristles 0.8–2.2 mm. long having thickened mineralized bases, or sometimes also minutely scabrous to villulose and cinereous; lower surfaces scabrous along the midrib; petioles very short, elliptic or somewhat rectangular, abaxial surfaces glabrous except for several large pungent bristles, rarely also villulose, the margins densely ciliate with long and short bristles, giving a white cottony appearance to the basal area of the leaf clusters on the lower surfaces. Flowers axillary, solitary or few. Calyces villous and ciliate, 3.0–4.0 mm. long; lobes lanceolate, free 2/3–3/4 the length, with large bristles 0.5–1.0 mm. long at the apices. Corollas pink, sometimes white, pale blue, or purple, 4.0–7.5 mm. long; the buds villulose. Stamens adnate to the corolla-tubes ca. 2/5 the length from base to limb. Styles 1.7–3.3 mm. long, cleft 1/13–1/3 the length. Nutlets (Figure 9C) 1–4, obpyriform, 1.5–2.0 (2.2) mm. long, (0.7) 0.8–1.1 mm. broad, indurated, dark brown to black with minute white and brown pustules, the attachment scars open, 0.3–0.5 mm. across at the apices, extending well below the middle. Chromosome number, $n = 9$.

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[2]Johnston (1923) designated Lincoln Co. as the type locality; however, McVaugh & Fosberg (1941) list Muddy Creek Valley in Clark Co., and no similar names in Lincoln Co. According to maps consulted by the present author Muddy River and Muddy Mountains are located in Clark Co.

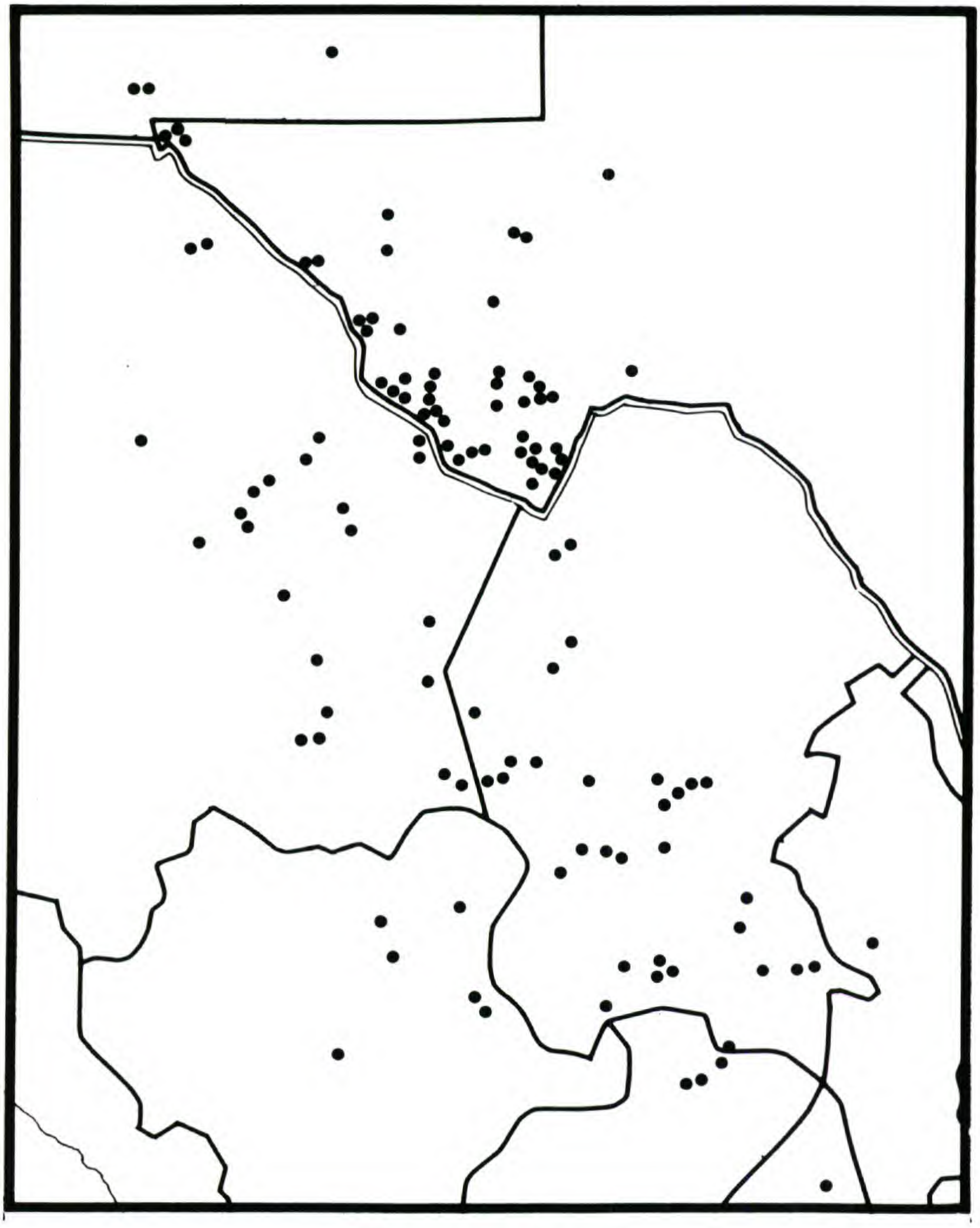

Figure 12. Distribution of *Tiquilia greggii*.

DISTRIBUTION: *Tiquilia latior* grows in red sandy soil, clay flats, and gypsum sand in the Colorado and Little Colorado River basins in Arizona, Nevada, and Utah (Figure 13) in association with *Astragalus, Atriplex, Ephedra, Juniperus, Larrea, Phacelia,* and *Stanleya.* It is geographically sympatric with *Tiquilia canescens, T. nuttallii,* and *T. plicata,* but it has not been reported growing with any of these species.

Flowering season is March through September.

The Supai Indians call this plant Ka-áw. They boil the roots to make a tea which they drink for stomach trouble (*Clover 5262,* GH).

Johnston (1923) treated *Tiquilia latior* as a foliar variation of *T. hispidissima* with a consistently wider leaf. The two taxa are treated here as separate species because they are disjunct and have diverged morphologically. The two taxa are, in most cases, more easily distinguished morphologically than are *T. hispidissima* and *T. gossypina,* which were recognized and contrasted by Johnston (1961). The morphological characetrs presented in the above key can be used to distinguish the two species.

For an objective evaluation, the mean, standard deviation, and standard error for nutlet length were calculated for each species, using measurements from 81 collections of *Tiquilia latior* and 80 collections of *T. hispidissima,* avoiding duplication of collections from the same locality. At a confidence level of 99%, the mean nutlet length for *T. hispidissima* will lie between 1.26 and 1.34 mm., and the mean nutlet length for *T. latior* will lie between 1.74 and 1.84 mm.

4. **Tiquilia hispidissima** (Torrey & Gray) A. Richardson, Sida **6:** 236. 1976.

Eddya hispidissima Torrey & Gray, Senate Executive Doc. No. 78, 33rd Congr., 2nd Sess. **2:** 170, 171. *Pl. 9.* 1857. TYPE: Common on the Rio Grande about El Paso, 1852, *Wright 1557.* (Lectotype fragment #2, GH! Duplicate of lectotype fragment #2, GH!).

Coldenia hispidissima (Torrey & Gray) Gray, Proc. Am. Acad. **5:** 340. 1862.

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 6.0 dm. broad from woody taproots (Figure 14); caudices to 1.5 cm. thick; young branches hispidulous-appressed with occasional spreading bristles. Leaves (Figure 6D) in clusters on short, brittle branches, 4.0–8.0 mm. long, 0.5–2.0 mm. broad; blades linear, occasionally narrowly lanceolate; upper surfaces usually green,

prickly with large bristles 0.5–2.4 mm. long having thickened mineralized bases, sometimes scabrous and lightly cinereous; lower surfaces scabrous along the midrib; petioles very short, elliptic or somewhat rectangular, glabrous, sometimes minutely scabrous, with pungent bristles along the margins. Flowers axillary, solitary. Calyces 2.5–4.0 mm. long, ciliate or villous with scattered sharp bristles 0.9–1.5 mm. long; lobes narrowly triangular or subulate, free 1/2–3/4 the length, inner surfaces lined with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; pink, rarely purple or white, with yellow throats; the tubes sometimes cylindrical, 2.5–6.5 mm. long; the buds villulose. Stamens adnate to the corolla tubes ca. 1/2 the length from base to limb. Styles 1.5–4.2 mm. long, cleft 1/10–1/4 the length. Nutlets (Figure 9D) 1–4, ovoid, 1.0–1.5 (1.7) mm. long, 0.7–1.1 (1.2) mm. broad, somewhat indurated, yellow to brown or sooty with white pustules ventrally, white-colliculate dorsally, the attachment scars open, 0.3–0.4 mm. across at the apices, extending well below the middle. Chromosome number, $n = 9$.

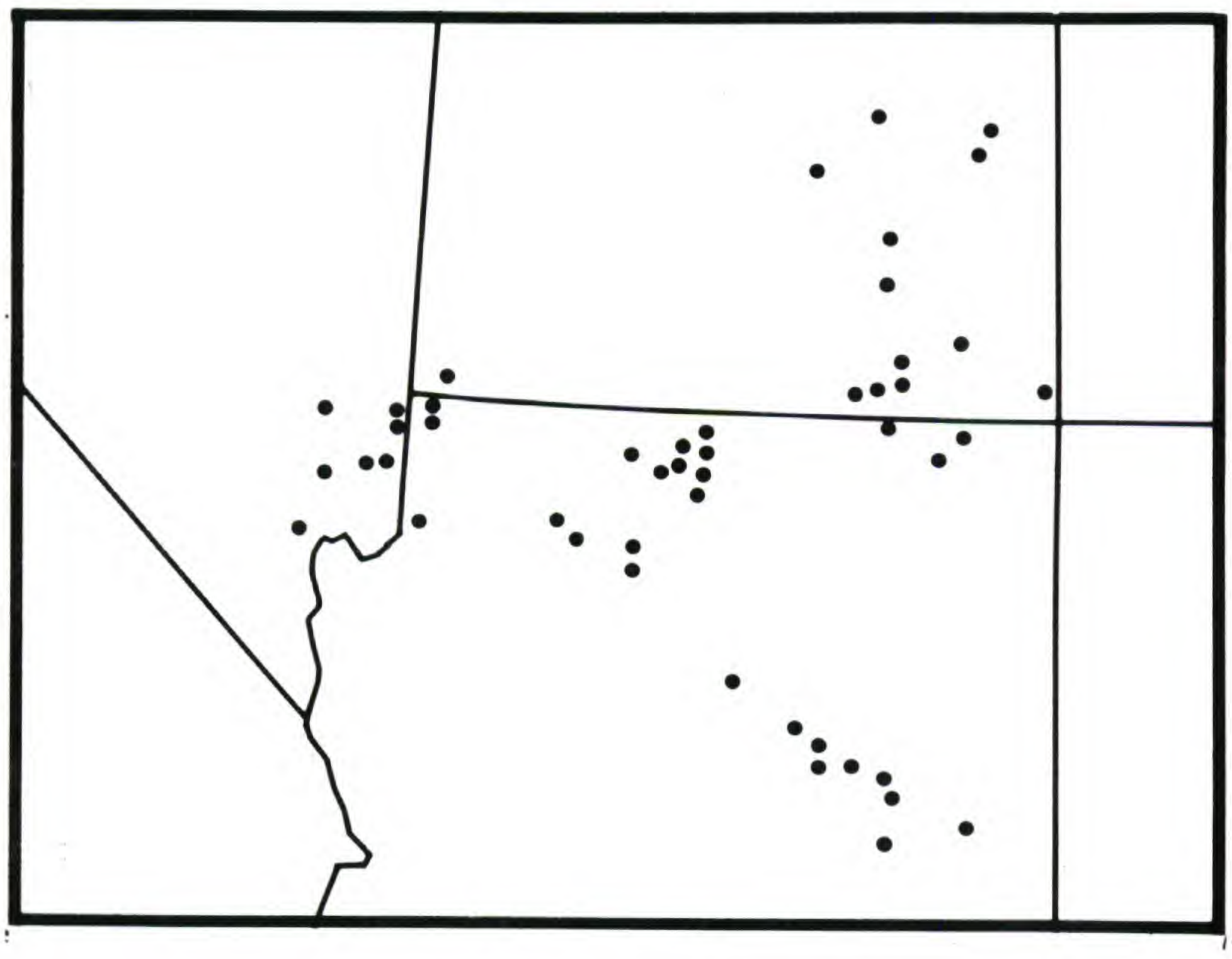

Figure 13. Distribution of *Tiquilia latior*.

Wright 1557 (GH) is a mixed collection of *Tiquilia hispidissima* and *T. gossypina.* The description and the accompanying illustrations contain elements of both species although both more closely correspond with *T. hispidissima.* On both herbarium specimens from the Gray Herbarium, fragment #1 is *T. gossypina* and fragment #2 is *T. hispidissima.* Consequently fragment #2 (GH) is designated the lectotype. A third herbarium specimen exists of *Wright 1557* (F!) but this has only *T. gossypina* and is eliminated as a type.

DISTRIBUTION: *Tiquilia hispidissima* occurs mainly in gypseous soils, occasionally calcareous soils in xeric regions of central New Mexico and trans-Pecos Texas, and in Mexico in eastern Chihuahua and western Coahuila (Figure 15). It grows in association with *Argemone turnerae, Bouteloua breviseta,* and species of *Atriplex, Chilopsis, Dasylirion, Fouquieria, Gutierrezia, Juniperus, Larrea, Nerisyrenia, Opuntia, Prosopis, Selinocarpus, Sporobolus, Suaeda,* and *Yucca.* It has been found *in situ* with 4 other species of *Tiquilia: T. canescens, T. gossypina, T. greggii,* and *T. mexicana;* and it is geographically sympatric with *T. tuberculata* and *T. turneri.*

This species flowers April through January.

Tiquilia hispidissima is distinguished from *T. gossypina* by the usually green, linear leaves with the petioles glabrous or scabrous but never villous; by the unappendaged corollas; and by the yellow to sooty nutlets with broad attachment scars. Comparisons with *T. latior* are made in the discussion of that species.

5. **Tiquilia tuberculata** A. Richardson, Sida **6:** 237. 1976. TYPE: **Mexico:** NUEVO LEON. Km. 100 on hwy. from Monterrey to Monclova, 28 Aug. 1973, *Richardson 2181.* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MEXU! MICH! NY! RM! UC! US!).

Small, gnarled and twisted subshrubs to 2.0 dm. tall and 3.0 dm. across, the caudices to 0.8 cm. thick; young stems densely villous and woolly to moderately villous. Leaves (Figure 6E) on short, brittle branches, 2.8–4.5 mm. long, 0.6–1.2 mm. broad; blades linear to oblong, upper and lower surfaces green, with large bristles 0.8–2.2 mm. long, rarely lightly cinereous and minutely hispid with hairs ca. 0.2 mm. long; petioles very short, elliptic or somewhat rectangular, minutely ciliate, abaxial surfaces glabrous or rarely lightly villous. Flowers axillary, solitary. Calyces 2.0–2.5 mm. long, ciliate, with occasional stiff bristles to 0.5 mm. long; lobes narrowly tri-

angular to subulate, free ca. 2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; lilac to milk-white, 4.5–6.0 mm. long; the buds glandular. Stamens adnate to the corolla tube ca. 1/3 the length from base to limb, veins below the point of attachment not winged. Styles 2.5–3.2 mm. long, cleft 1/5–1/2 the length. Nutlets (Figure 9E) 1–4, ovoid, 1.0–1.1 mm. long, 0.5–0.6 mm. broad, black with white tubercles, the attachment scar slightly open, 0.1–0.15 mm. across at the apex, tapering to a point along a ridge ca. half way to the base, the ridge continuing to the base.

DISTRIBUTION: Two populations ca. 20 km. apart are known, both from northwestern Nuevo Leon, Mexico (Figure 16). *Tiquilia tuberculata* grows in gypseous soils in association with *Fouquieria, Frankenia, Larrea, Lycium, Nerisyrenia, Opuntia, Selinocarpus, Sporobolus,* and *Suaeda.* It is geographically sympatric with *Tiquilia canescens, T. mexicana,* and *T. turneri,* but it has not been reported to be growing in mixed populations with any of these species.

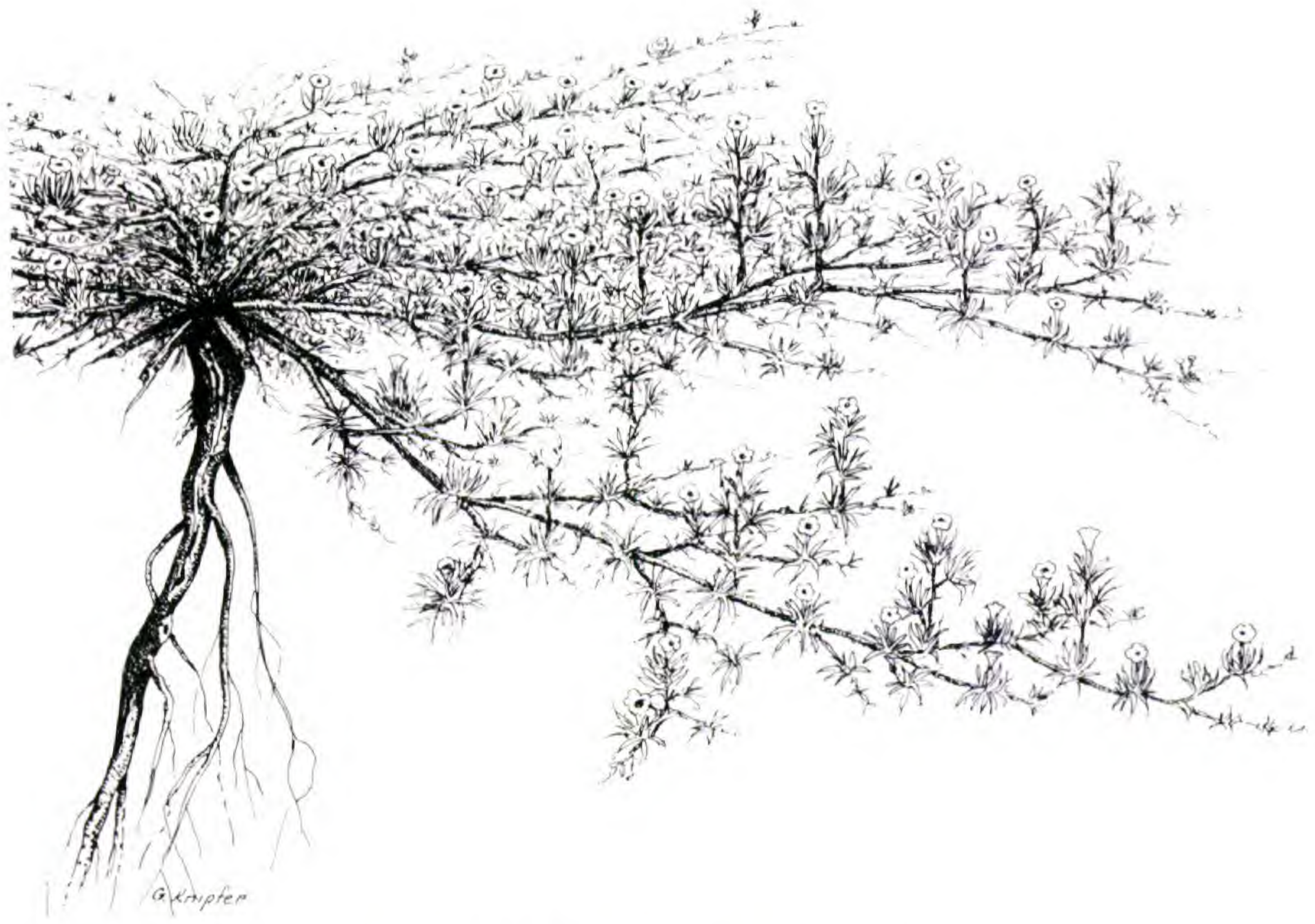

Figure 14. Drawing of habit of *Tiquilia hispidissima.*

Flowering times, known from limited collecting data, are March, July, and August.

The most outstanding characteristic of this species is the white-tuberculate ornamentation on the nutlets. In all other species of *Tiquilia* the nutlets are aculeate, colliculate or pusticulate, granulate, or lacking in ornamentation. Nutlet and floral characters are the most convenient in distinguishing *T. tuberculata* from *T. gossypina* and *T. turneri.*

6. **Tiquilia turneri** A. Richardson, Sida **6:** 237, 238. 1976. TYPE: **Mexico:** COAHUILA. 12.4 mi. S and 2 mi. W of Cuatro Ciénegas, in gypsum dunes, 29 Jun. 1971, *Richardson 1595.* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MEXU! MICH! NY! RM! UC! US!).

Gnarled and twisted subshrubs (Figure 17) forming mounds to 9.0 dm. across, the caudices to 10.0 cm. thick; juvenile forms procumbent; young stems densely villous and woolly to moderately villous; leaf clusters on short brittle branches, the internodes between the branches on old plants sharply reduced in length and hidden by the leaf clusters. Leaves (Figure 6F) 2.5–5.5 mm. long, 0.6–1.5 mm. broad; blades linear to oblong; upper and lower surfaces densely villous and cinereous to lightly villous and green, with large bristles 0.7–1.7 mm. long; petioles very short, elliptic or somewhat rectangular, heavily villous over all or ciliate. Flowers axillary, solitary. Calyces 2.0–3.0 mm. long, densely villous or ciliate; lobes narrowly triangular to subulate, free ca. 1/2 the length, each with soft antrorsely appressed hairs on the inner surface and with 1 or 2 stiff apical bristles 0.7–1.7 mm. long. Corollas opening in the morning and falling in the evening; violet with yellow throats, 3.4–6.5 mm. long; the buds glandular. Stamens adnate to the corolla tube ca. 1/3 the length from base to limb, the veins winged below the point of attachment. Styles 1.5–3.3 mm. long, cleft 1/6–1/2 the length. Nutlets (Figure 9F) 1 or 2, ovoid, 0.8–1.5 mm. long, 0.6–0.8 mm. broad, shiny black, smooth or granular, not indurated, the attachment scars slightly open, 0.1–0.15 across at the apex, tapering to a point at the base. Chromosome number, $n = 9$.

The specific epithet is given in recognition of B. L. Turner who first collected this taxon and called it to my attention.

DISTRIBUTION: Two populations, separated by about 160 kilometers, are known (Figure 16). The first to be known grows in and around shifting gypsum dunes about 25 km. southwest of Cuatro Ciénegas, Coahuila, Mexico, where it is the dominant plant growing with *Dasylirion, Nerisyrenia, Selinocarpus,* and *Yucca.* The second population grows in a gypseous area about 100 km. northwest of Monterrey, Nuevo Leon, Mexico, the dominant plant growing with *Dyssodia acerosa, Tiquilia mexicana,* and species of *Larrea, Opuntia,* and *Yucca.* Although *Tiquilia turneri* has been observed growing with only one other species of *Tiquilia* (*T. mexicana*), it is geographically sympatric with *T. canescens, T. gossypina,* and *T. greggii.*

This species flowers May through October.

There are two distinct growth forms, depending on the age of the plants and possibly the substrate. Old shrubby plants, which grow to 9.0 dm. across and 4.0 dm. high with caudices to 10.0 cm. diameter, are found in the gypsum dunes near Cuatro Ciénegas. They show marked reduction in internode length, bringing the leaf clusters close together and hiding the stem. There is a reduction in leaf size (2.5–4.5 mm. long) and length of bristles on the leaves and calyces (0.7–1.0 mm. long), and there is an abundance of fine appressed hairs giving the leaves a cinereous appearance and completely covering the young stems giving a white woolly appearance.

Younger plants growing near the base of the same gypsum dunes are herbaceous and prostrate, growing to 4.0 dm. across, with slightly larger leaves (to 5.5 mm. long), longer internodes (0.5–1.0 cm. long), and longer bristles (1.0–1.7 mm. long) on the leaves and calyces. The leaves are usually green because of reduced pubescence; the petioles are villous to glabrous; and the fine hairs only partially cover the young stems.

The Nuevo Leon population is much like that of the gypsum dunes in Coahuila. The plants are small subshrubs with larger leaves, less pubescence, and slightly smaller nutlets.

Tiquilia turneri is closely related to *T. gossypina,* the two species having several floral and vegetative characters in common. *Tiquilia turneri* is distinguished from *T. gossypina* by its smaller leaves and flowers, the shrubby habit and often reduced stem internodes, and the smaller and somewhat narrower nutlets which have a thin and relatively soft and smooth pericarp.

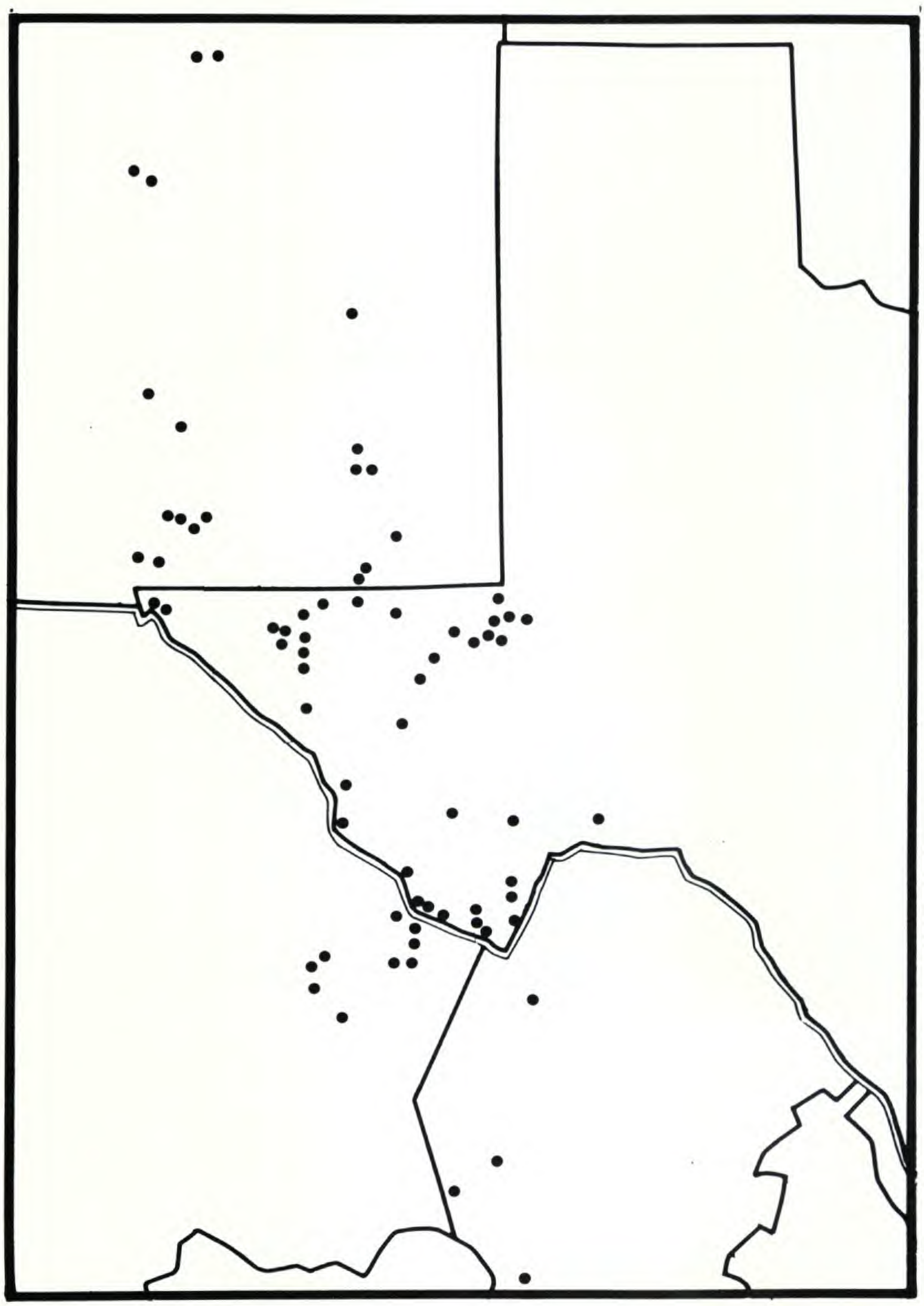

Figure 15. Distribution of *Tiquilia hispidissima*.

7. **Tiquilia mexicana** (Watson) A. Richardson, Sida **6:** 236. 1976.

Coldenia mexicana Watson, Proc. Am. Acad. **18:** 120. 1883. TYPE: **Mexico:** COAHUILA. In the mountains east of Saltillo, Aug. 1880, *Palmer 872.* (Holotype, GH! Isotypes, F! NY! US!).

Coldenia tomentosa Watson, Proc. Am. Acad. **18:** 120. 1883. TYPE: **Mexico:** COAHUILA. In the Sierra Madre 40 mi. south of Saltillo, Mar. 1880, *Palmer 864.* (Holotype, GH! Isotype, US!).

Coldenia mexicana var. *tomentosa* (Watson) I. M. Johnston, Wrightia **2:** 159. 1961.

Herbaceous, procumbent, forming mats to 1 meter across from woody caudices; caudices to 1.0 cm. thick; branches cinereous, densely villous, with occasional stiff bristles to 1.0 mm. long. Leaf blades (Figure 6G) ovate to elliptic, 6.0–10.5 mm. long, 2.5–5.3 mm. broad, upper and lower surfaces cinereous and densely villous (rarely lightly villous and green), with stiff bristles 1.0–2.0 mm. long with thickened mineralized bases; petioles filiform distally, broader near the base, 1.6–6.0 mm. long, villous, with spreading bristles to 1.2 mm. long. Flowers axillary, solitary, or in small bracteate clusters. Calyces 3.0–4.0 mm. long, densely villous or ciliate, with scattered sharp bristles to 1.0 mm. long; lobes lanceolate to subulate, free 2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning, falling in the evening; purple, violet or pink, often with a yellow throat, 5.0–9.0 mm. long; the buds glabrous, glandular, or villulose. Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, the veins below the points of attachment swollen or rarely winged. Styles 2.4–4.7 mm. long, cleft 1/4–1/2 the length. Nutlets (Figure 9G) 1 or 2, rarely 3, ovoid, 1.0–1.5 mm. long, 0.7–1.1 mm. broad, black with white collicula, the attachment scars slightly open to 0.2 mm., only above the middle. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia mexicana* occurs in southern trans-Pecos Texas, eastern Chihuahua, Coahuila, western Nuevo Leon, and northern Zacatecas (Figure 18), where it grows in both limestone and gypseous soils, always in xeric conditions and without evident competition, with the exception of other species of *Tiquilia.* It is often found growing with *T. canescens, T. gossypina, T. greggii, T. hispidissima,* and *T. turneri,* and is geographically sympatric with *T. purpusii* and *T. tuberculata.* It grows in association with *Agave, Flourensia, Fouquieria, Larrea, Opuntia,* and *Prosopis.*

Flowering season is February to November.

In Mexico, it is known as Oreja de Ratón.

Watson (1883) described *Coldenia tomentosa* as resembling *C. mexicana* but with thicker, more strongly revolute leaves, shorter petioles, and larger flowers and nutlets. These characters vary, and intermediate conditions are commonly found. Johnston (1961) recognized *C. mexicana* var. *tomentosa,* acknowledging only one sharp, decisive character, the villulose condition of the bud in the var. *tomentosa.* This character is variable, even within populations. Therefore *Tiquilia mexicana* is treated here as a variable species with no subdivisions.

Tiquilia mexicana has some characters in common with *T. gossypina,* in particular the nutlet characters, but it is distinguished from that species by its wider leaves, longer and slender petioles, and its herbaceous habit. The two species grow together and no hybrids have been detected.

8. **Tiquilia gossypina** (Wooton & Standley) A. Richardson, Sida **6:** 236. 1976.

Eddya gossypina Wooton & Standley, Contr. U. S. Nat. Herb. **16:** 164. 1913. TYPE: **New Mexico:** DONA ANA CO. Tortugas Mountain, Las Cruces, 2 Sep. 1894, *Wooton s.n.* (Holotype, US No. 690234. Fragment of holotype with photograph of holotype, GH!).

Coldenia gossypina (Wooton & Standley) I. M. Johnston, Wrightia **2:** 158. 1961.

Herbaceous to suffrutescent, procumbent to decumbent, forming mats to 6.0 dm. across from woody taproots; caudices to 1.5 cm. thick; young branches scabrous, strigose, or hispid. Leaves (Figure 6H) 3.3–11.7 mm. long, 0.6–2.3 mm. broad; blades narrowly obovate, sometimes linear; upper surfaces cinereous, occasionally light green, villous or scabrous, prickly with large bristles 0.8–2.0 mm. long having thickened mineralized bases; lower surfaces scabrous, especially along the prominent midribs, usually also villous, rarely glabrous; petioles very short, elliptic or somewhat rectangular, usually villous, sometimes glabrous and shiny brown on abaxial surfaces, with large pungent bristles at the margins. Flowers axillary, solitary. Calyces 2.0–3.7 mm. long, villous or ciliate, with scattered sharp bristles to 1.7 mm. long; lobes narrowly triangular to subulate, free 1/2–2/3 the length, inner surfaces with antrorsely appressed hairs. Corollas opening in the morning and falling in the evening; purple to pink or rarely white, with yellow throats, 4.3–11.5 mm. long; the buds glabrous or glandular.

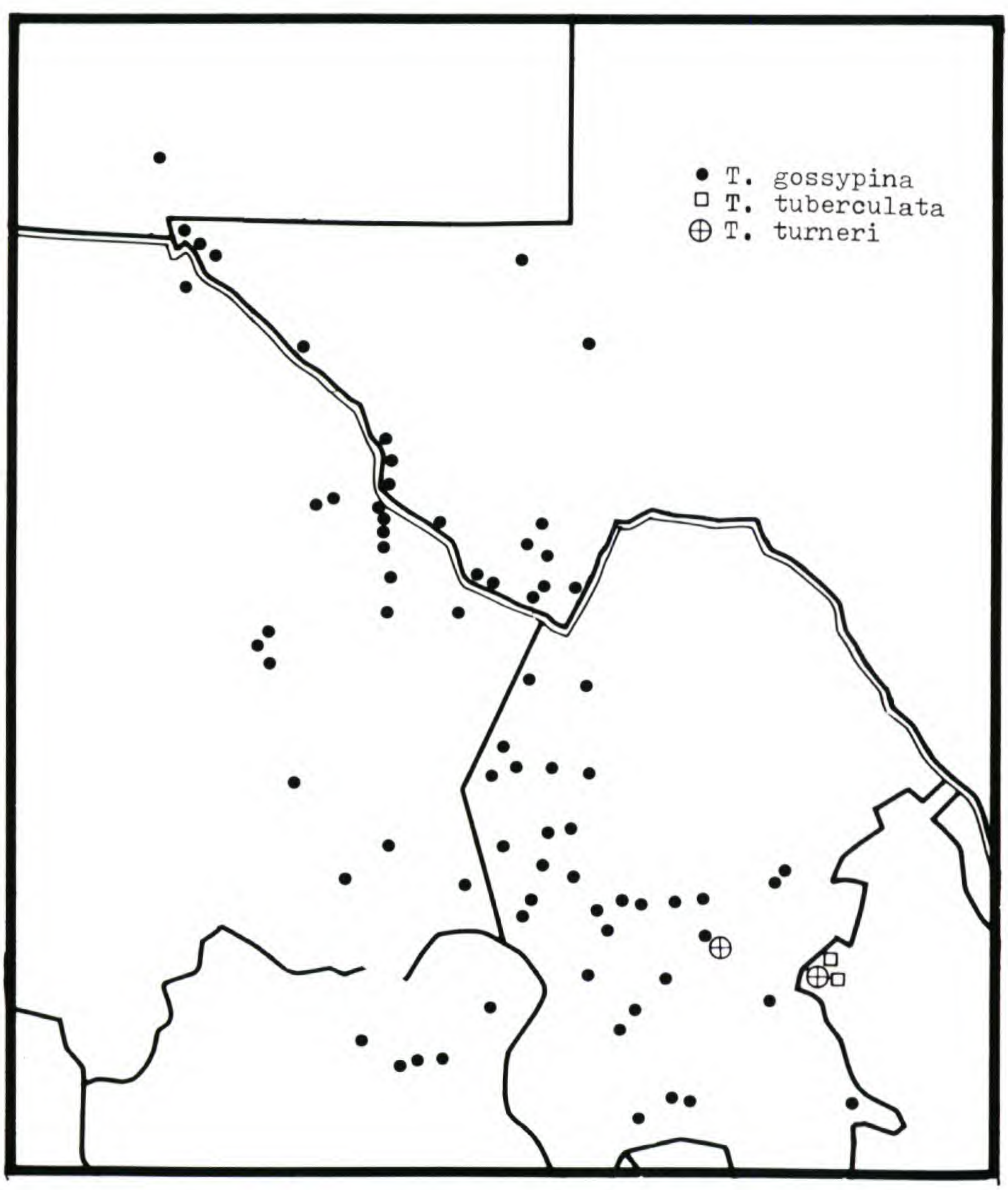

Figure 16. Distribution of *Tiquilia gossypina*, *T. tuberculata*, and *T. turneri*.

Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, the veins below the points of attachment winged. Styles 2.1–6.5 mm. long, cleft 1/4–1/3 the length. Nutlets (Figure 9H) 1–4, ovoid, (0.9) 1.1–1.3 (1.5) mm. long, (0.7) 0.8–1.0 (1.3) mm. broad, somewhat indurated, black with white pustules ventrally, white-colliculate dorsally, the attachment scars slightly open, to 0.2 mm., only above the middle. Chromosome number, $n = 9$.

DISTRIBUTION: *Tiquilia gossypina* occurs in southern New Mexico, and adjacent trans-Pecos Texas, especially near the Mexican border; in Mexico it occurs in eastern Chihuahua, Coahuila, and northern Durango (Figure 16), in association with *Fouquieria, Larrea, Nama, Nerisyrenia, Selinocarpus,* and *Yucca.* It usually grows in gypseous soils and competes only with other species of *Tiquilia.* It is often found growing with *T. canescens, T. greggii, T. hispidissima,* and *T. mexicana.* This investigator has seen it growing in the same clump with *T. canescens* and *T. hispidissima,* all flowering, and it is geographically sympatric with *T. purpusii* and *T. turneri.*

Tiquilia gossypina flowers March through November. It appears to be less gypsum-tolerant than *T. hispidissima, T. tuberculata,* and *T. turneri.* Suffrutescent forms are often found in areas of high gypsum concentration, although growing alongside herbaceous forms. The suffrutescence is usually correlated with a marked reduction in leaf size.

A dimorphic population of *Tiquilia gossypina* was found growing along the roadside in Coahuila, Mexico, 40 kilometers north of Monclova. One hundred samples were taken for populational studies, 50 from each side of the highway (*Richardson 1643A & 1643B*). Two distinct forms were growing intermingled, with no intergradation observable in the field. One form was typical *T. gossypina;* the other showed a marked vegetative similarity to *T. hispidissima.*

Morphological studies in the laboratory showed a uniformity of size, shape, color, and ornamentation of the nutlets among all samples, corresponding with *Tiquilia gossypina.* Essential floral characters were also those of *T. gossypina.* The nutlet and floral characters have proved to be reliable within the genus, whereas the vegetative characters are often variable. Therefore, in the absence of experimental data, both forms must be referred to *T. gossypina,* although the possibility that the plants represent F_1 hybrids cannot be ruled out.

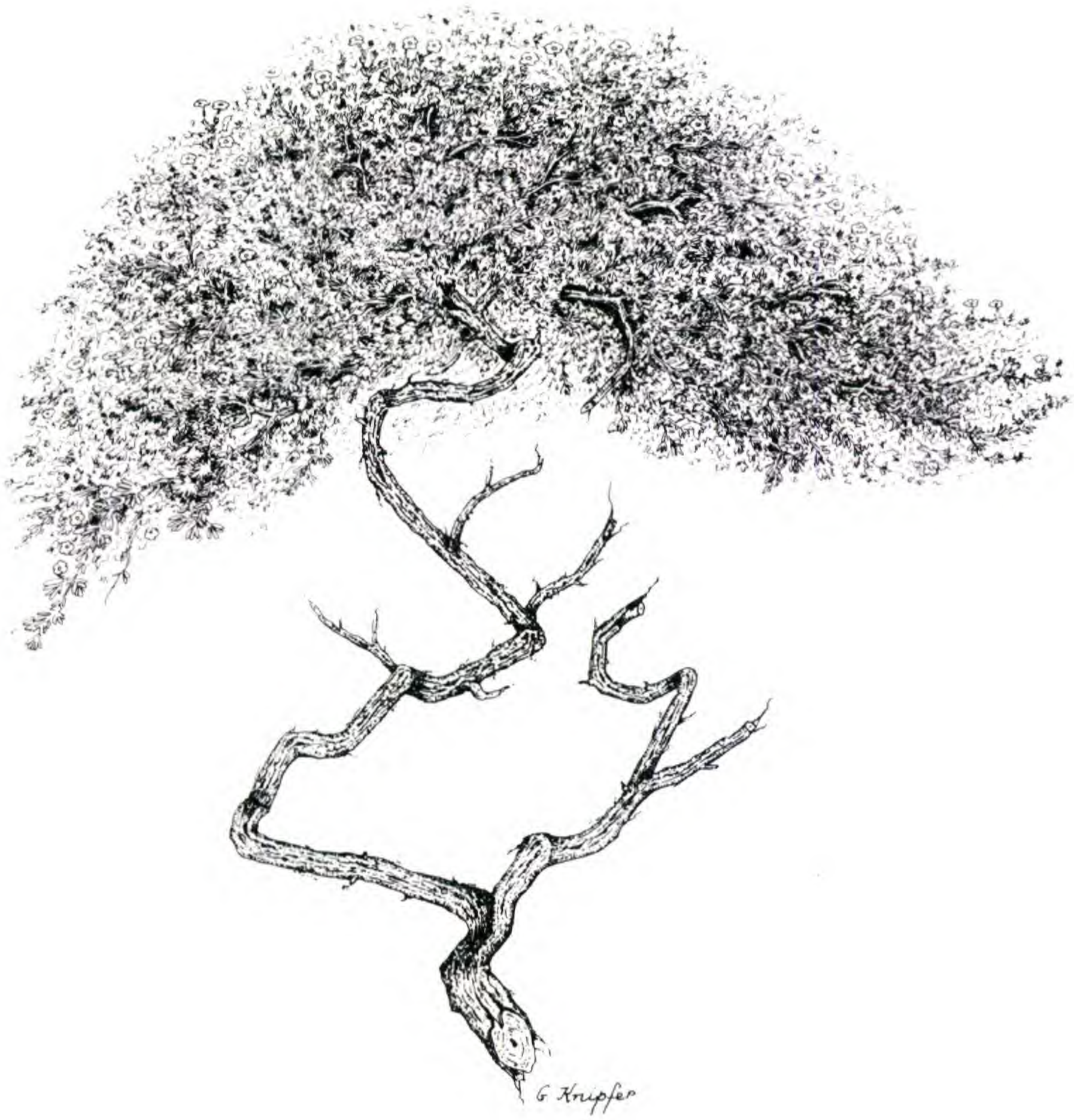

Figure 17. Drawing of habit of *Tiquilia turneri*.

Several populations in southern Chihuahua and northern Durango are in question (*Correll & Johnston 20228, Gentry 8628, Johnston 7762, Juzepczuk 637, Ripley & Barneby 13953, Shreve 8790*). Field studies of these populational sites were not made; therefore, all observations were necessarily made from preserved herbarium material. Typical *Tiquilia gossypina* has not been collected with these populations, although it has been collected in nearby parts of Chihuahua and Durango.

These populations are uniform, vegetatively like *Tiquilia hispidissima* in the extreme. This evidently influenced Johnston to identify his collections as forms related to *T. hispidissima*. The

floral parts, however, are those of *T. gossypina* and the nutlets, although not identical with *T. gossypina,* are quite like this species. Neither the floral nor the nutlet characters resemble *T. hispidissima.* Field studies and experimental work are needed to clarify the relationships of these populations. For the present they are included with *T. gossypina.*

Tiquilia gossypina is best distinguished from *T. hispidissima,* with which it has often been confused, by (1) its black nutlets with narrow attachment scar; (2) the glabrous or glandular condition of the bud; (3) the winged condition of the veins below the stamen attachment to the corolla; and (4) the usually villous condition of the petiole.

9. **Tiquilia purpusii** (Brandeg.) A. Richardson, Sida **6:** 237. 1976.

Coldenia purpusii Brandeg., Univ. Calif. Publ. Bot. **4:** 186. 1911. TYPE: **Mexico:** SAN LUIS POTOSÍ. Minas de San Rafael, Nov. 1910, *Purpus 4857* (Holotype, UC! Isotypes, F! GH! US!).

Herbaceous and procumbent, forming mats to 6.0 dm. across from woody caudices; caudices to 1.2 cm. thick; branches with abundance of fine spreading hairs to 1.2 mm. long, often also villulose. Leaf blades (Figure 6I) green, narrowly ovate to ovate, 5.0–10.0 mm. long, 1.5–5.5 mm. broad; upper surfaces with fine, antrorsely inclined bristles to 1.2 mm. long with thickened, mineralized bases, midveins somewhat sunken, lateral veins not conspicuous; lower surfaces with higher concentration of bristles and with midveins and lateral veins prominent; petioles filiform, 1.5–6.5 mm. long, densely covered with stiff, spreading hairs to 1.2 mm. long, giving a white cottony appearance to the petiole area of the leaf clusters on the lower surfaces. Flowers axillary and solitary or several, or in small clusters subtended by bracts. Calyces persistent, 3.0–5.5 mm. long with an abundance of slightly antrorsely inclined stiff bristles to 1.0 mm. long, especially toward the base; lobes narrowly triangular, free ca. 3/4 the length, with short antrorsely appressed hairs on the inner surfaces. Corollas opening in the morning and falling in the evening; light blue to amethyst with darker throats, rarely ivory-white, 5.0–7.2 mm. long; the buds glabrous, minutely glandular and villous, or with spreading bristles to 0.2 mm. long. Stamens adnate to the corolla tubes ca. 1/4 the length from base to limb, the veins below the points of attachment usually swollen, sometimes faintly winged. Styles 2.2–4.9 mm.

long, cleft 1/8–1/4 the length. Nutlets (Figure 9I) 1–4, usually 1 or 2, often arranged spirally in the fruit, ovoid, 0.9–1.4 mm. long, 0.6–0.9 mm. broad, dark brown to slate-gray with white collicula, the attachment scars slightly open above the middle, to 0.1 mm. wide and 0.3 mm. long, the suture running obliquely to the base. Chromosome numbers, $n = 9$; $n = 8$.

DISTRIBUTION: *Tiquilia purpusii* has the southernmost distribution of the North American species of *Tiquilia*, excepting for the widespread *T. canescens* (Figure 19). It grows in xeric sites in Mexico, occurring in southeastern Coahuila, southern Nuevo Leon, Querétaro, San Luis Potosí, southwestern Tamaulipas, and northeastern Zacatecas, in association with *Cordia, Jatropha, Larrea, Nama, Prosopis, Yucca,* and various grasses on gypseous or limestone soils. It is occasionally found competing successfully with grasses but usually does not grow in close proximity with other plants. *Tiquilia purpusii* grows with one other species of *Tiquilia, T. canescens,* and is geographically sympatric with *T. gossypina, T. greggii,* and *T. mexicana* at its northern limits of distribution.

Flowering seasons are January through March and June through December.

Among the species of southwestern United States and central Mexico, *Tiquilia purpusii* is notable for its bright green leaves and its nutlets with oblique sutures. The collicula are relatively larger on the nutlets of this species, and the exocarp is often a slate-gray color. Vegetatively, it resembles *T. cuspidata* of Sonora and Baja California, but the fruit characters are quite different. (*Tiquilia cuspidata* has black, granular nutlets with long, straight, wide attachment scars and with basally attached styles.) The species is quite distinct and is not likely to be confused with another.

Tiquilia subgen. **Tiquilia.** TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

Leaf margins entire or crenate. Nutlets ovoid, hemiovoid, or spheroid, smooth, minutely colliculate, minutely aculeate, or granular, the ornaments always smaller than 0.04 mm. across. Style attachments apical, sub-apical, sub-basal, or basal. Chromosome number, $n = 8$ (rarely aneuploid with $n = 9$), 16, 15, & 14.

Tiquilia sect. **Tiquiliopsis** Gray, Proc. Am. Acad. **5:** 340. 1862. TYPE SPECIES: *Tiquilia nuttallii* (Bentham ex Hooker) A. Richardson.

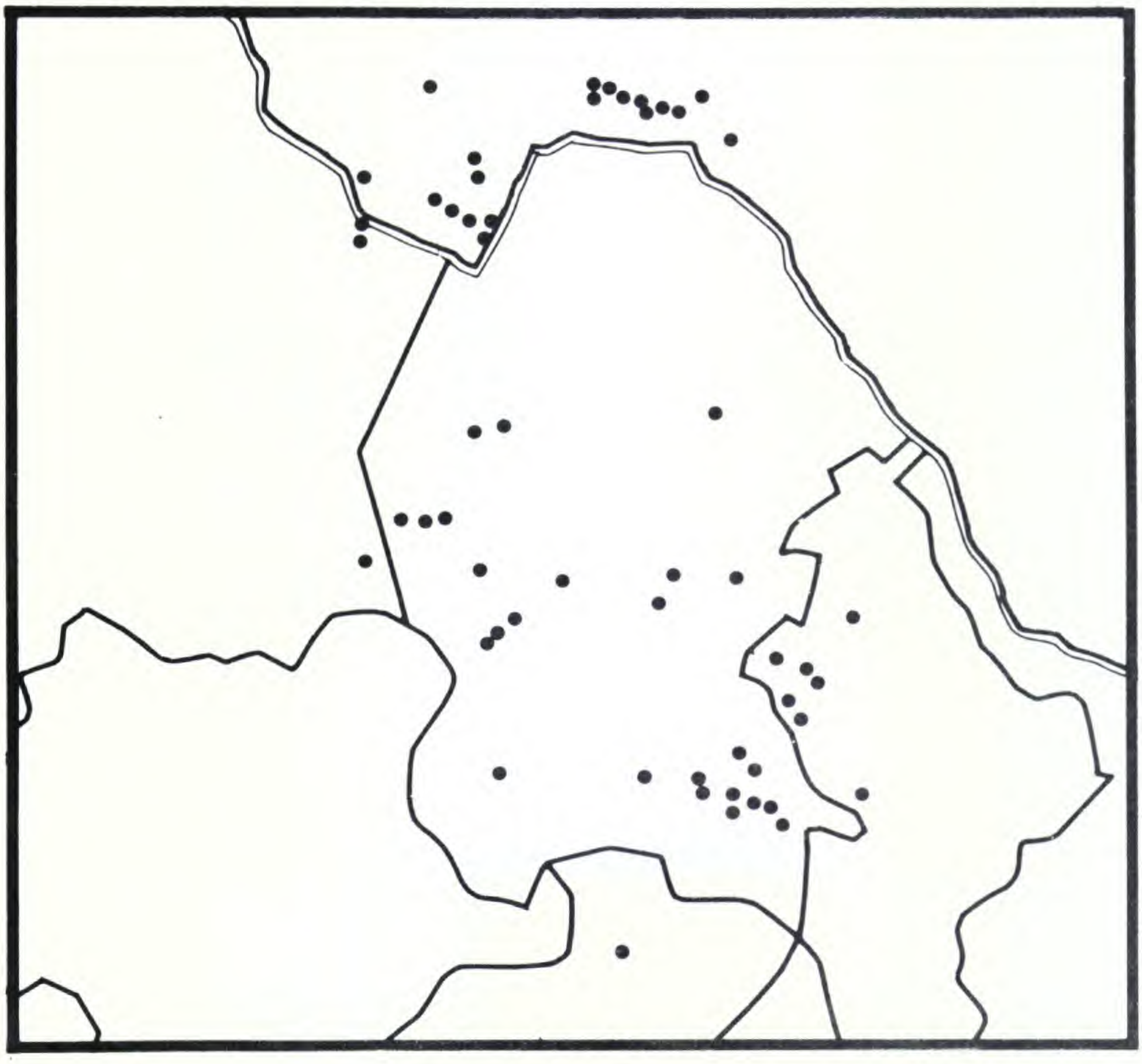

Figure 18. Distribution of *Tiquilia mexicana*.

Plants procumbent or spreading, herbaceous from woody caudices. Leaves in axillary or terminal clusters; blades elliptic, lanceolate, ovate-obovate or sub-orbicular, marginally entire. Flowers in clusters with the leaves. Calyces persistent. Corollas deciduous. Stamens unequal, included, adnate to the corolla tubes at 3 levels. Style attachments sub-apical, sub-basal, or basal. Fruits lobed, of 1–4 nutlets; nutlets ovoid or spheroid, indurated, smooth, granular, or minutely aculeate. Chromosome number, $n = 8$ (*Tiquilia palmeri* with aneuploids $n = 9$).

This section includes four species; three of them North American, in western United States and western Mexico; and one amphitropical disjunct species which occurs in western North America and again in South America, western Argentina.

KEY TO THE SPECIES OF TIQUILIA SECT. TIQUILIOPSIS

a. Leaf blade without crowded, deeply plicate lateral veins; nutlet smooth, granular, or minutely aculeate, brown or black, dull or shiny; style attachment sub-apical or basal. ..... b.
  b. Petiole filiform; nutlet brown or mottled grey, brown, and black, smooth or minutely aculeate. ..... c.
    c. Lateral veins of leaves at ca. 30° angle to the midrib; corolla 3.0–4.0 mm. long; style not exserted beyond calyx lobes, attachment sub-apical; nutlet ovoid. ..... 10. *T. nutallii.*
    c. Lateral veins of leaves at ca. 45° angle to the midrib; corolla 3.5–9.5 mm. long; style exserted beyond calyx lobes, attachment basal; nutlet spheroid. ..... 13. *T. palmeri.*
  b. Petiole ovate-trullate, sometimes filiform distally; nutlet black, granular. .. .. 12. *T. cuspidata.*
a. Leaf blade with 4–7 pairs of crowded, deeply plicate lateral veins; nutlet smooth, black, shiny; style attachment sub-basal. ..... 11. *T. plicata.*

10. **Tiquilia nuttallii** (Bentham ex Hooker) A. Richardson, Sida **6:** 236. 1976.

Coldenia nuttallii Bentham ex Hooker, Hooker's Jour. Bot. Kew Gard. Misc. **3:** 296. 1851. TYPE: **Utah:** UTAH CO. Sandy desert of muddy rivers near the great salt-lake Timpanagos (sic.), Aug. 1845, *Geyer 80.* (Holotype, K! Isotypes, K! TEX!).

Tiquilia parvifolia Nuttall ex Hooker, Hooker's Jour. Bot. Kew Gard. Misc. **3:** 296. 1851, *nomen. nud.* (A reference to a Nuttall manuscript.)

Tiquilia brevifolia Nuttall ex Torrey, Bot. Wilkes Exped. **2:** 410. 1874. TYPE: On the Walla-Walla River, Washington Territory (Holotype, GH!).

Tiquilia oregana Torrey, Bot. Wilkes Exped. **2:** 410. 1874, *nomen. nud., lapsus calami.*

Tiquiliopsis nuttallii (Bentham) Heller, Muhlenbergia **2:** 239. 1906.

Coldenia decumbens Hauman, Apuntes Hist. Nat. **1:** 55. 1909. TYPE: **Argentina:** MENDOZA. Terrenos arenosos del valle del Rio Tupungato, a 2500 metros de altitud, no lejos de Punta de Vacas, a principios de febrero de 1908, *L Hauman 268.* (Holotype, BA! Possible isotype, GH!.) (Herbarium label on holotype indicates 2350 meters altitude.)

Coldenia nevadensis Gand., Bull. Soc. Bot. France **65:** 61. 1918. TYPE: **California:** Ad Reno, 5 June 1894, *Hillman s.n.* (Holotype, LY! Isotypes, POM! RM!).

Procumbent or spreading, forming mounds to 3.0 dm. across; caudices to 0.5 cm. thick; older stems woody, the bark pale brown; young branches villous or pubescent with stiff appressed hairs to 0.2 mm. long, with scattered spreading or inclined bristles to 1.2 mm. long. Leaves (Figure 6J) in clusters at the nodes or stem apices; blades green or gray-green, ovate to elliptic, 3.8–9.5 mm. long, 2.2–7.8 mm. broad, with 2–3 pairs of lateral veins ascending

ca. 30° from the midrib; upper surfaces strigose and with scattered or abundant large antrorsely inclined bristles to 1.0 mm. long, especially along veins and margins; lower surfaces more densely pubescent with finer spreading or appressed hairs to 0.5 mm. long; petioles filiform, 2.5–8.5 mm. long, with abundant spreading hairs to 1.7 mm. long. Flowers in bracteate clusters, Calyces 2.5–4.0 mm. long, outer surfaces glistening, with short inclined or appressed hairs 0.1–0.3 mm. long, and larger spreading or antrorsely inclined bristles 0.5–1.5 mm. long; lobes narrowly triangular, free 2/3–3/4 the length, often ciliate, inner surfaces with antrorsely appressed hairs. Corollas white to violet with yellow throats, 3.0–4.0 mm. long, the tubes often constricted near the apices or rarely cylindrical; the buds glabrous or glandular. Stamens adnate to the corolla tubes ca. 1/3 the length from base to limb, veins below stamen attachments winged near bases of tubes, wings ca. 0.5 mm. long. Styles 1.0–2.3 mm. long, not exserted beyond the calyx, cleft 1/2–3/4 the length, attached to the nutlets sub-apically, 0.3–0.4 mm. below the nutlet apices. Nutlets (Figure 9J) 4, oblong-ovoid, 1.1–1.5 mm. long, 0.6–0.8 mm. broad, shiny and smooth (minutely colliculate under high magnification), gray, mottled brown or black. Cotyledons hippocrepiform (Gray, 1888). Chromosome number $n = 8$.

DISTRIBUTION: *Tiquilia nuttallii* occurs in northern Arizona, eastern and southern California, northwestern Colorado, southern Idaho, Nevada, eastern Oregon, Utah, eastern Washington, and southwestern Wyoming (Figure 20). It is usually found growing in desert sands or sandy loam, from below sea level to 2400 meters altitude, with associations of *Artemisia, Atriplex, Chrysothamnus, Juniperus, Larrea,* and *Pinus.* It grows with *T. palmeri* and *T. plicata* and is geographically sympatric with *T. canescens* and *T. latior.* Two collections, from north central New Mexico and Missouri, are no doubt recent introductions.

Tiquilia nuttallii is also found in South America (Figure 21) in northwestern Argentina in the provinces of Mendoza and San Juan. It occurs at altitudes of 1500–3050 meters, in sand and sandy clay in association with *Adesmia, Ephedra, Gilia, Glandularia, Hoffmanseggia, Larrea, Lycium, Nama, Senecio, Stevia, Stipa, Verbena,* and various cacti.

Tiquilia nuttallii has the southernmost distribution of the South American species and is the only species of *Tiquilia* known east of

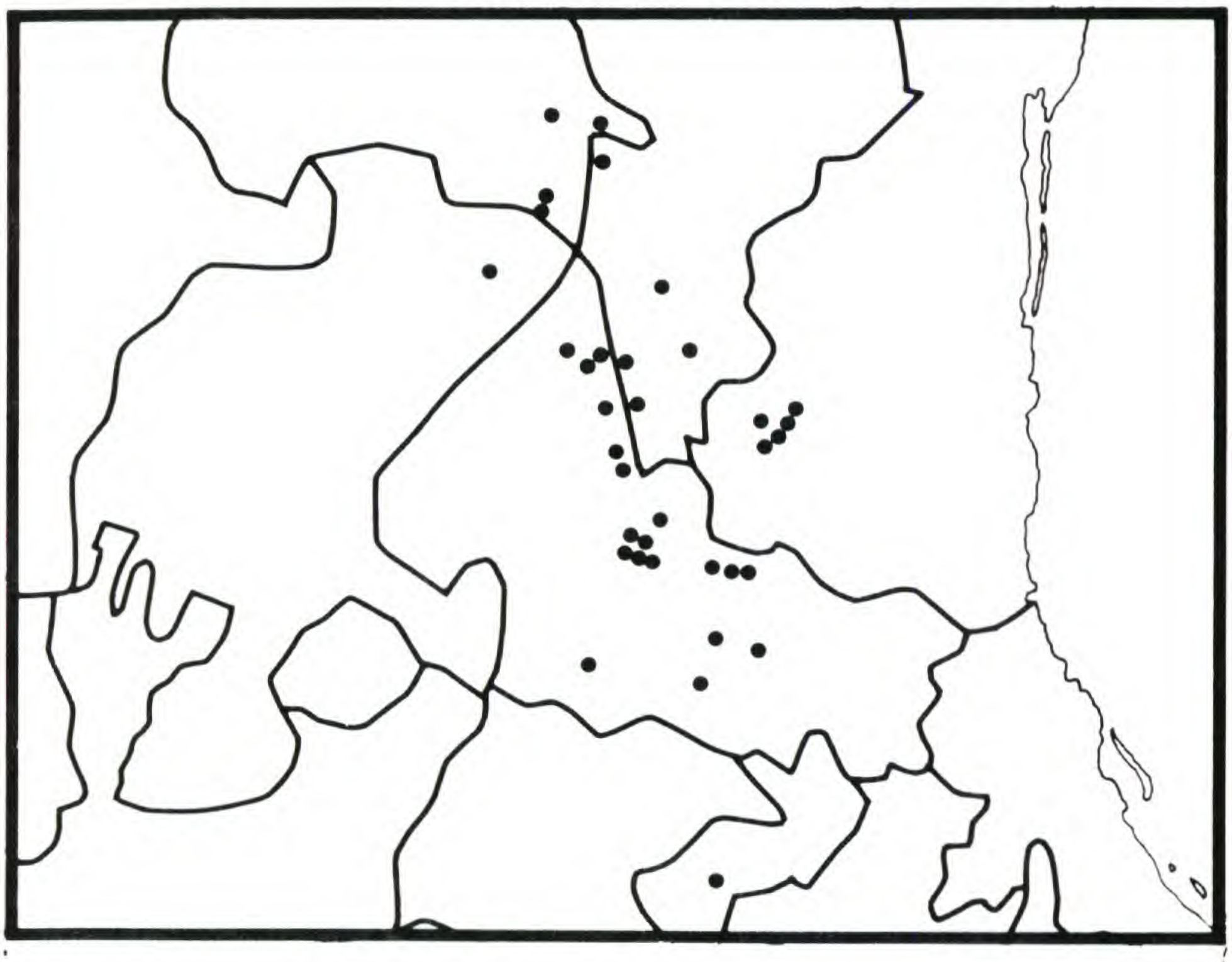

Figure 19. Distribution of *Tiquilia purpusii*.

the Andes. It is also the only species found on both American continents. It is the northernmost species in North America, reaching near the Canadian border in its northern extreme. Considering the broad intracontinental and intercontinental distribution of this species, it is remarkably uniform, the North and South American plants being indistinguishable morphologically.

Tiquilia nuttallii flowers March through September in North America, and November through March in South America.

Tiquilia nuttallii is sometimes confused with *T. palmeri,* with which it grows in the southern limits of its distribution in North America. The two species are most easily distinguished by the characters presented in the accompanying key.

11. **Tiquilia plicata** (Torrey) A. Richardson, Sida **6:** 237. 1976.

Tiquilia brevifolia var. *plicata* Torrey, *In* United States and Mexican Boundary Survey **2:** 136. 1859. TYPE: **California:** Desert west of the Colorado, 28 Nov. 1846, *Lt. Emory s.n.* (Holotype, NY! Photograph, GH!).

Coldenia plicata (Torrey) Coville. Contr. U. S. Nat. Herb. **4:** 163. 1895.

Procumbent or spreading, forming mounds to 6.0 dm. across and 1.5 dm. tall, producing new shoots from underground rhizomes; caudices to 3.0 mm. thick; older stems woody with light brown bark; young branches with fine antrorsely appressed and spreading hairs to 0.7 mm. long. Leaves (Figure 6K) in nodal or apical clusters; blades green, obovate to ovate, 4.5–13.6 mm. long, 2.5–8.0 mm. broad, deeply plicate, 4–7 pairs of crowded lateral veins; upper surfaces with fine appressed hairs converging on the medians between the veins and flowing toward the margins, hairs along margins antrorsely appressed, also with scattered bristles to 0.6 mm. long with thickened mineralized bases; lower surfaces with fine dense spreading and inclined hairs to 0.4 mm. long; petioles filiform, 2.5–11.0 mm. long, with dense antrorsely inclined hairs to 0.7 mm. long. Flower clusters ebracteate. Calyces 2.5–3.0 mm. long, outer and inner surfaces with ascending hairs to 1.0 mm. long, very dense on lower half of inner surfaces; lobes subulate, free nearly to the base. Corollas white, pink, blue, violet, or purple, often with yellow throats, the throats sometimes apically constricted, 3.5–6.0 mm. long; the buds glabrous or glandular. Stamens adnate to the corolla tubes ca. 2/7 the length from base to limb, the veins below stamen attachments often faintly winged or with scales near base of tube. Styles 2.2–3.0 mm. long, cleft 1/2–4/5 the length, attached to the nutlets sub-basally, 0.2–0.3 mm. above the base, exserted beyond the calyces. Nutlets (Figure 9K) 3–4, ovoid to broadly ovoid, 0.8–1.0 mm. long, 0.5–0.7 mm. across, smooth, black and shiny. Chromosome number, $n = 8$.

DISTRIBUTION: Eastern Arizona, southern California, southern Nevada, and adjacent Baja California and Sonora (Figure 22). *Tiquilia plicata* is usually found in desert or beach sands or sandy gravel, from 71 meters below sea level to 770 meters above sea level with associations of *Ambrosia, Atriplex, Baccharis, Cercidium, Ephedra, Larrea, Opuntia, Populus,* and *Prosopis.* It grows in mixed populations with *T. palmeri* and is geographically sympatric with *T. canescens, T. cuspidata, T. latior,* and *T. nuttallii.*

This species flowers February through December.

Tiquilia plicata is the only species known to have underground rhizomes. It is recognized easily by its deeply plicate leaves with 4–7 pairs of lateral veins, and its smooth and shiny black ovoid nutlets with sub-basal style attachment.

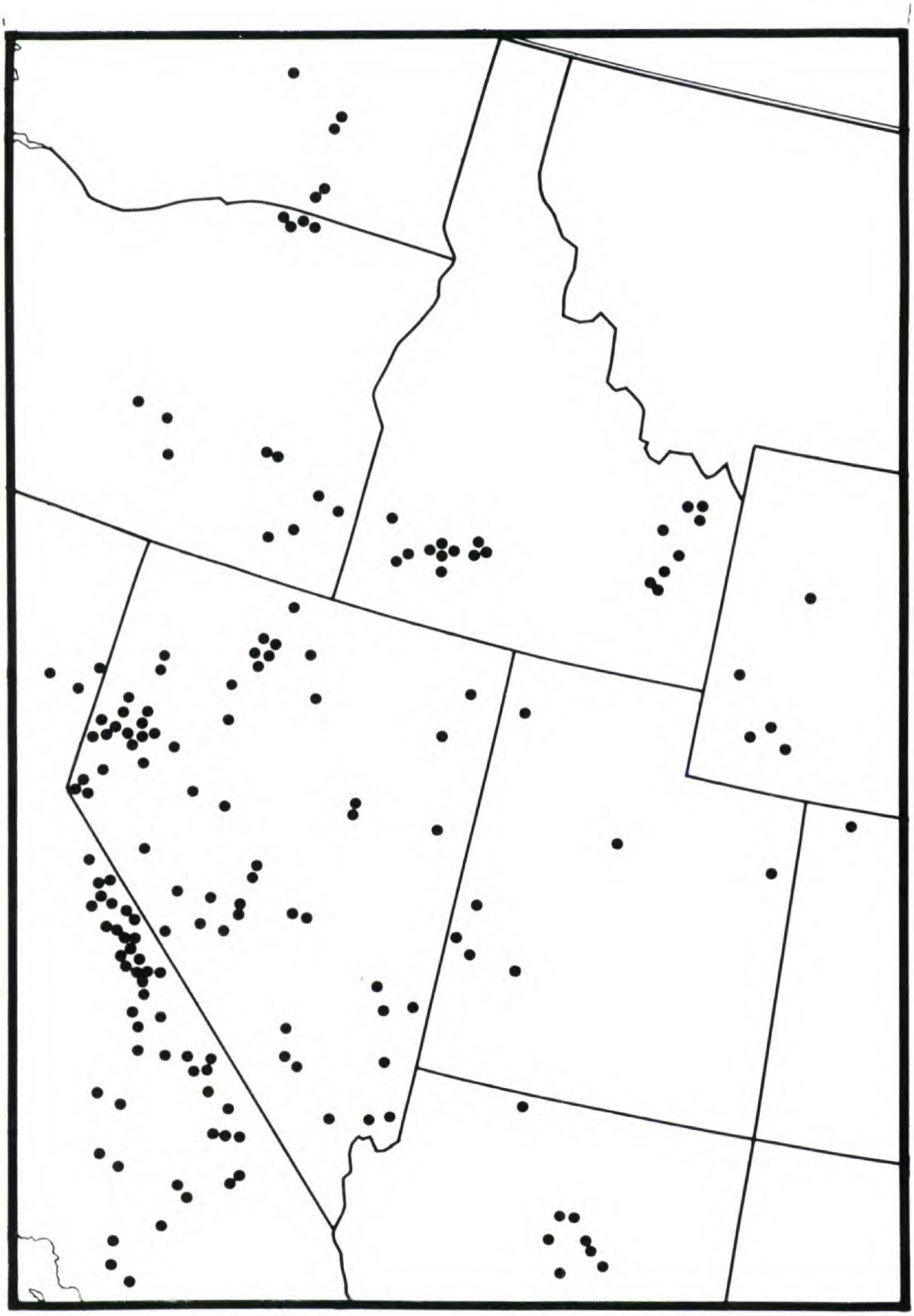

Figure 20. Distribution of *Tiquilia nuttallii*, North America.

12. **Tiquilia cuspidata** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia cuspidata I. M. Johnston, Proc. Calif. Acad. IV. **12:** 1137–1140. 1924. TYPE: **Mexico:** In gypsum soil on San Marcos Island, Gulf of California, 12 May 1921, *Johnston 3617* (Holotype, CAS! Isotypes, GH! NY! UC! US!).

Coldenia loretensis M. E. Jones, Contr. W. Bot. **18:** 65. 1933. TYPE: **Mexico:** Baja California. Mts. east of Loreto, 17 Oct. 1930, *Jones 27394* (Holotype, POM! Isotypes, GH! NY! RSA! UC! US!).

Procumbent or spreading, forming mounds to 6.0 dm. across and 2.0 dm. tall; caudices to 10.0 mm. thick; older stems woody with gray to light brown bark; young stems villous or with spreading hairs to 0.5 mm., sometimes hoary. Leaves (Figure 6L) in clusters on short branches or stem apices; blades green to cinereous, ovate, the apex acute with a pungent bristle, 3.5–6.0 mm. long, 1.7–4.0 mm. broad; upper surfaces sparsely to densely pubescent with antrorsely appressed or inclined hairs to 0.4 mm. long, some thicker with mineralized bases, usually more dense basally; lower surfaces with spreading or antrorsely inclined hairs to 0.4 mm. long with thickened mineralized bases especially along veins and margins; petioles ovate-trullate, sometimes filiform distally, 1.5–4.0 mm. long; abaxial surfaces of basal portions with spreading or inclined stiff hairs to 0.5 mm. long, the margins densely ciliate giving a white cottony appearance to the basal portion of lower surfaces of leaf clusters; filiform portions, when present, with spreading bristles to 1.0 mm. long. Flower clusters bracteate. Calyces ca. 2.0 mm. long, with stiff spreading or inclined hairs to 0.5 mm. long; lobes narrowly triangular, free half the length or slightly less, inner surfaces lined with antrorsely appressed hairs. Corollas white tinged bluish or lilac, the throats yellowish green, 3.5–7.0 mm. long; the buds villulose. Stamens adnate to the corolla tubes ca. 2/5 the length from base to limb, the veins below stamen attachments faintly winged most of the length. Styles 1.8–2.5 mm. long, cleft 2/5–3/4 the length, exserted beyond the calyces; attached basally and adnate to the nutlets ca. 3/4 the length, this portion at maturity visible only as a membranous tissue on the nutlet (style lengths given do not include the adnate portion). Mericarps usually 1, sometimes 2, rarely 4. Nutlets (Figure 9L) 1, rarely 2 with the remaining ovules absent or aborting, black and granular; ovate 1.1–1.4 mm. long, 0.7–0.9 mm. broad, attachment scars tapering from 0.3 mm. across at the base to a point ca. 0.4 mm. below the apex. Chromosome number, $n = 8$.

DISTRIBUTION: Mexico, mainly Baja California, also Sonora (Figure 23). *Tiquilia cuspidata* is usually found in sandy desert habitat, often near the Gulf of California, and has been collected in gypseous soils. It grows with *Beloperone californica, Cercidium microphyllum, Cereus giganteus, Dalea emoryi,* and species of *Ferocactus, Fouquieria, Jatropha, Larrea, Lycium, Pachycereus* and *Prosopis.* It is geographically sympatric with *T. palmeri* and *T. plicata,* but has not been reported growing with either of these.

Flowering seasons are January through May and August through November.

Tiquilia cuspidata, with its ovate-trullate petioles, ovate-acute leaf blades, and black granular nutlets with basal style attachments cannot be readily confused with any other North American species of *Tiquilia.* An outstanding character not seen in any other member of the genus is the reduction in number of mericarps. Number of nutlets is further reduced by abortion. Abortion of mericarps, although not uncommon, is a consistent condition in only a few species.

Similarities of nutlet characteristics with those of some species in section *Galapagoa* are considered parallel evolution resulting from selection in similar habitats.

13. **Tiquilia palmeri** (A. Gray) A. Richardson, Sida **6:** 236. 1976.

Coldenia palmeri Gray, Proc. Am. Acad. **8:** 292. 1870. TYPE: **SE California** or **Arizona,** on the lower Colorado, 1869, *Palmer s.n.* (Holotype, GH! Fragment of holotype, fragment #1, UC! Probable isotype, US! Possible isotypes, NY! US!).

Coldenia brevicalyx Watson, Proc. Am. Acad. **24:** 62. 1889. TYPE: On the lower Colorado, 1869, *Palmer s.n.* (Holotype, GH! Fragment of holotype, fragment #1, UC! Probable isotype, US! Possible isotypes, NY! US!).

Coldenia angelica Watson, Proc. Am. Acad. **24:** 62, 63. 1889. TYPE: **Mexico:** BAJA CALIFORNIA. Los Angeles Bay, Gulf of California, 1887, *Palmer 517* (Holotype, US! Isotypes, ARIZ! GH! NY! NY! UC! US!).

Nama coldenioides M. E. Jones, Contr. W. Bot. **12:** 57. 1908. TYPE: **California:** SAN BERNARDINO CO. Needles, 10 May 1884, *Jones 3869* (Holotype, POM!).

Triquiliopsis palmeri (Gray) Rydb., Fl. Rocky Mountains and Adjacent Plains. New York. p. 711, 1917.

Procumbent or spreading, forming mounds to 9.0 dm. across, caudices to 1.4 cm. thick; older stems woody, bark whitish; young stems densely villous or with mostly antrorsely appressed or inclined hairs to 0.6 mm. long. Leaves (Figure 6M) in clusters or unequal pairs at the nodes and in apical clusters; blades gray-green to gray, ovate to suborbicular, sometimes elliptic in Sonora and

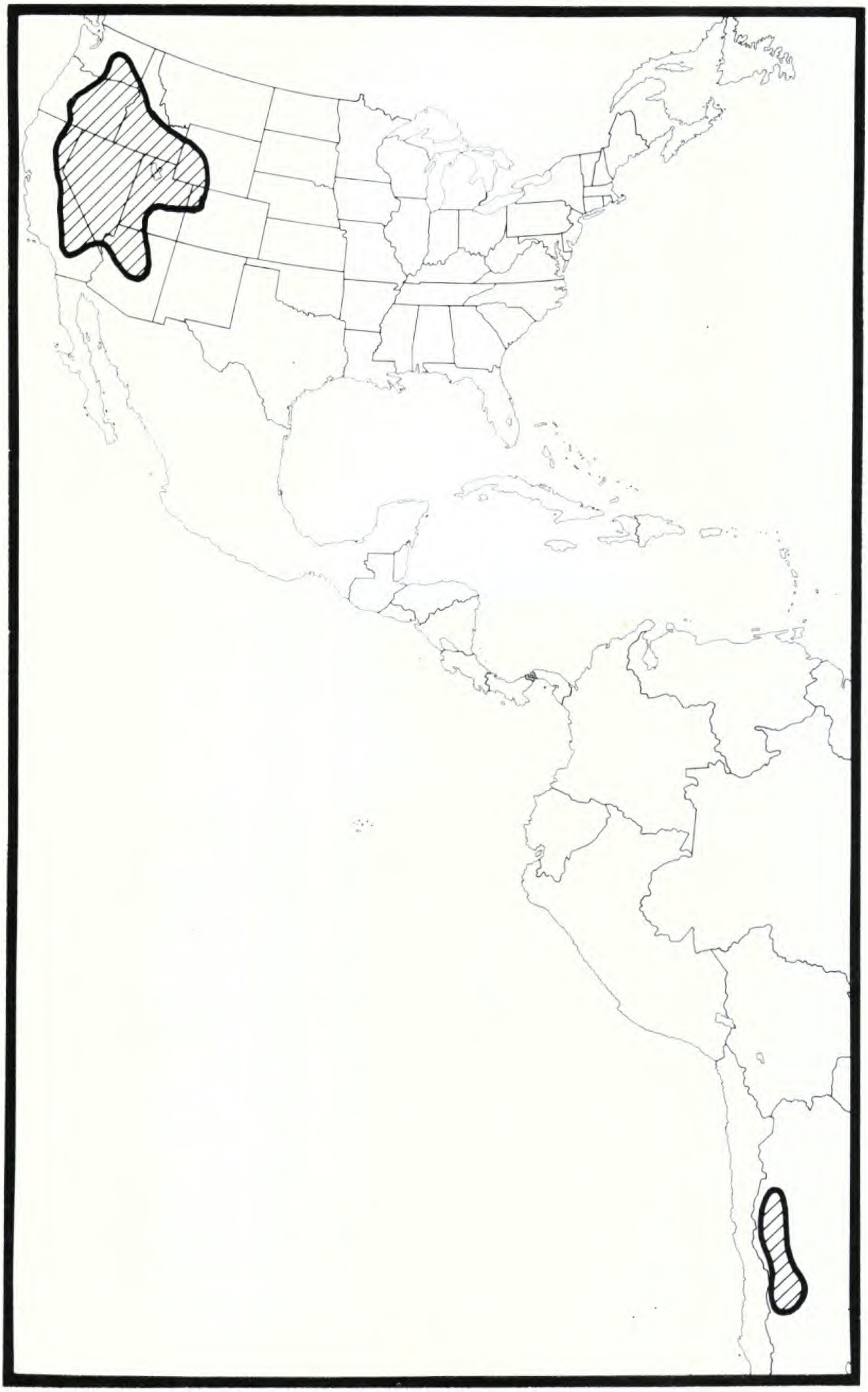

Figure 21. Distribution of *Tiquilia nuttallii*, North and South America.

Baja California, 3.0–14.5 mm. long, 2.5–9.5 mm. broad, with 2–3 pairs of lateral veins ascending at ca. 45° from the midvein, often plicate, margins often irregular; upper surfaces marginally or antrorsely appressed pubescent, hairs to 0.4 mm. long, with scattered spreading or inclined bristles, especially along the margins, to 1.0 mm. long; lower surfaces densely appressed, rarely spreading pubescent; petioles filiform, 2.0–16.0 mm. long, with appressed or spreading hairs to 0.6 mm. long. Flower clusters bracteate. Calyces 2.0–3.5 mm. long, lower half of outer surface with dense spreading or appressed hairs to 0.6 mm. long, upper half less densely pubescent with shorter hairs; lobes narrowly triangular, each with an apical bristle, free ca. half the length, inner surfaces with fine antrorsely appressed hairs. Corollas blue, lavender or purple, with yellow throats, 3.5–9.5 mm. long; the buds hispidulous or glandular. Stamens adnate to the corolla tubes ca. 2/5 the length from base to limb, the veins from the points of stamen attachment winged about half the distance to base of tubes. Styles 2.0–3.0 mm. long, cleft ca. half the length, exserted beyond the calyx lobes, attached to the nutlets basally. Nutlets (Figure 9M) 4, spheroid, 1.0–1.1 mm. across, smooth, brown and shiny, rarely black and minutely aculeate, attachment scars circular. Chromosome numbers, $n = 8$, and aneuploids $n = 9$.

Watson (1889) described *Coldenia brevicalyx* in an attempt to clarify a mixed collection of the holotype of *C. palmeri* Gray, assigning this new name to the entire mounted portion and most of the loose material in a packet on Gray's holotype. He assigned the name *palmeri* to a few loose leaves (actually from *Tiquilia plicata*), which were included in the packet of loose material. Gray (1870) believed these leaves to be from younger plants of the species he described. As stated by Johnston (1924a), it is unrealistic to believe Gray described the few loose leaves as *Coldenia palmeri* and ignored the bulk of the material. Thus, *C. brevicalyx* is an unnecessary renaming of *C. palmeri*.

DISTRIBUTION: Eastern Arizona, southern California, and southern Nevada, and adjacent Baja California and Sonora (Figure 24). *Tiquilia palmeri* is usually found in desert sands or in sand mixed with clay or gravel, from sea level to about 925 meters altitude with associations of *Agave, Ambrosia, Cercidium, Fouquieria, Ja-*

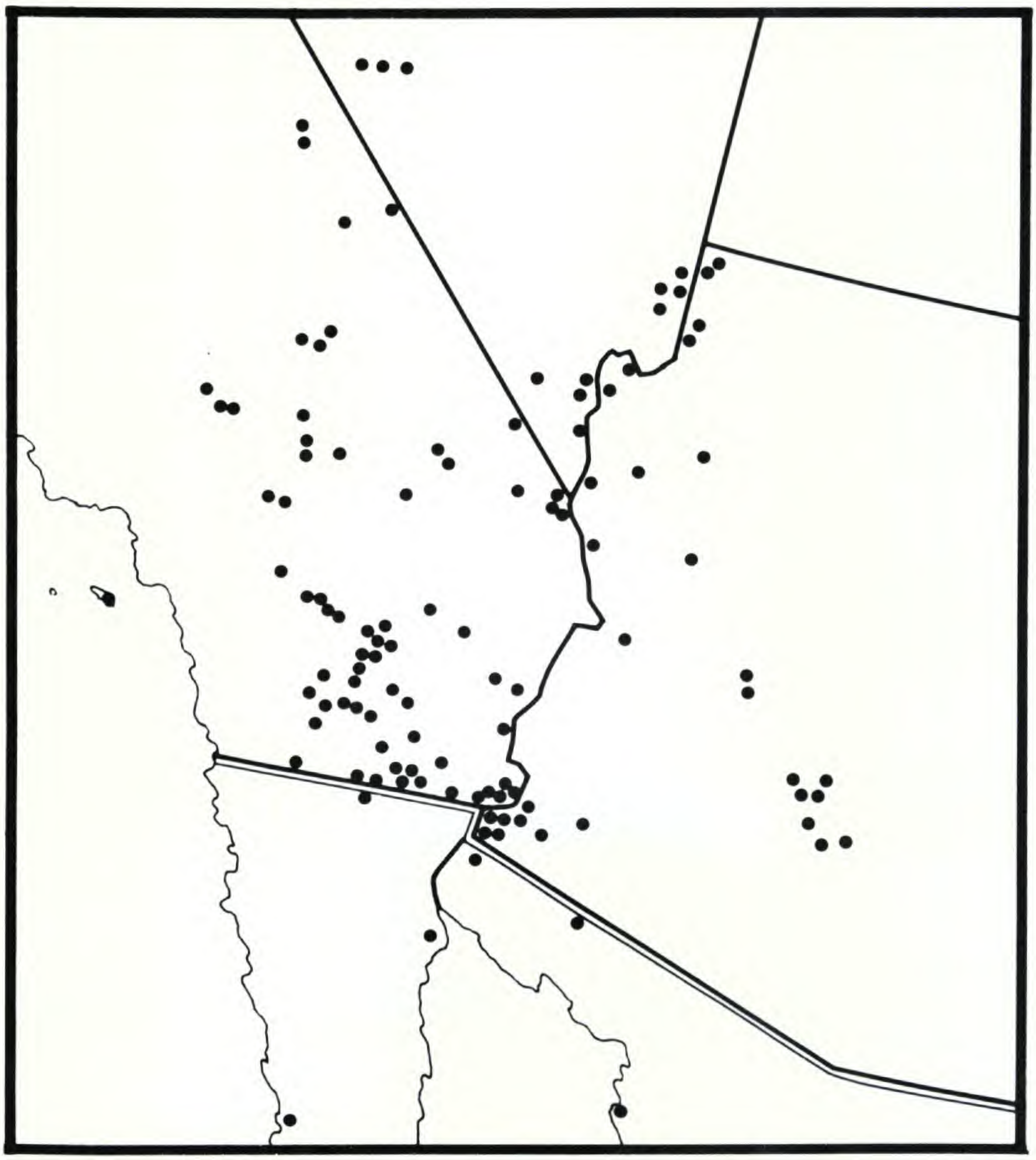

Figure 22. Distribution of *Tiquilia plicata.*

tropha, Larrea, Nicotiana, and *Prosopis.* It grows with *T. plicata* and is geographically sympatric with *T. canescens, T. cuspidata, T. latior,* and *T. nuttallii.*

This species flowers every month of the year, but in any fixed locality the period of active growth is limited.

Tiquilia palmeri is vegetatively similar to *T. nuttallii,* but is quite distinct from that species. The two species are compared in the discussion of *T. nuttallii.*

Tiquilia palmeri, with its spheroid nutlets and gynobasic styles, is reminiscent of the South American sect. *Sphaerocarya,* in particular, *T. conspicua,* the only member of that section with a gynobasic style. This situation must be considered a matter of parallel evolution in similar habitats.

Tiquilia sect. **Tiquilia.** TYPE SPECIES: *Tiquilia dichotoma* (Ruiz & Pavon) Persoon.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades narrowly ovate, ovate, or lanceolate, the margins entire or crenate; petioles linear or filiform. Flowers in clusters with the leaves or solitary at the nodes. Calyces persistent or deciduous. Corollas persistent, with invaginations forming prominent ridges below the stamen attachments. Stamens equal or unequal, exserted well beyond the corolla limbs (3.0–8.0 mm.), adnate equally or subequally to the corolla tubes. Style attachments apical. Fruits slightly lobed, of 1–4 nutlets. Nutlets more or less hemi-ovoid, the ventral surfaces broadly flattened, the convex dorsal surfaces and sides blotched grey, brown, and black, minutely colliculate. Chromosome number, $n = 16$.

This section includes four species in South America, in northern Chile and Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. TIQUILIA

a. Leaf blade deeply plicate, usually marginally crenate. ..... b.
  b. Nutlet with a knife-like collar surrounding the ventral surface; corolla 8.5–13.0 mm. long. ..... 16. *T. grandiflora.*
  b. Nutlet without a knife-like collar surrounding the ventral surface; corolla 5.0–6.0 mm. long. ..... 14. *T. dichotoma.*
a. Leaf blade not deeply plicate, marginally entire. ..... c.
  c. Nutlet ventral surface markedly narrowed and shortened by inrolling of carpel; corolla 7.5–10.0 mm. long; calyx indurated, retaining the nutlets, deciduous. ..... 17. *T. ferreyrae.*
  c. Nutlet ventral surface slightly narrowed by inrolling of carpel; corolla 4.5–5.5 mm. long; calyx not indurated, opening to release the nutlets, persistent. ..... 15. *T. simulans.*

14. **Tiquilia dichotoma** (Ruiz & Pavon) Persoon, Syn. Pl. **1:** 157. 1805.

Lithospermum dichotomum Ruiz & Pavon, Prodr. et Fl. Peruviana et Chilensis **2:** 5. *t. 111c.* 1799. TYPE: **Peru:** Lima. Sands toward Lurin, vicinity of the

village of Pachacámac, *Ruiz & Pavon 11/6* (Holotype, MA! Probable isotype, OXF).

Coldenia dichotoma (Ruiz & Pavon) Lehm., Plantae E Familiae Asperifoliarum Nuciferae **1:** 9. 1818.

Coldenia pentandra Juss. ex Steud., Nomenclator Bot. 212. 1821, *nomen. superfl.*, based on an unnamed specimen collected by *Dombey* (Probably *Dombey 364* GH!) and described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible congener of *Coldenia*.

Coldenia dombeyana Juss. ex DC., Prodr. Syst. Nat. **9:** 558. 1845, *nomen. superfl.*, based on an unnamed specimen collected by *Dombey* (Probably *Dombey 364* GH!) and described in passing by Jussieu, Gen. Pl. 130. 1789, as a possible congener of *Coldenia*.

Procumbent to semi-erect, forming mats to 20.0 dm. across; caudices to 8.0 mm. thick; older stems woody, bark whitish or brown; young stems with spreading hairs to 0.9 mm. long. Leaf blades (Figure 7A) green, oblong or ovate, 9.0–20.0 mm. long, 4.0–7.0 mm. broad, with 3–6 pairs of plicate lateral veins, the margins crenate; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, also with sparse antrorsely inclined bristles to 0.5 mm. long with thickened mineralized bases; lower surfaces with spreading hairs to 0.3 mm. long, especially along the veins; petioles filiform, 4.5–9.5 mm. long with spreading hairs to 1.0 mm. long, abruptly more dense basally. Flower clusters ebracteate. Calyces persistent, 3.5–5.0 mm. long, with antrorsely inclined hairs to 0.6 mm. long, especially along the lobe margins; lobes subulate, free 2/5–1/2 the length, each with 1 or 2 apical bristles to 0.5 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas lilac to milk-white color, 5.0–6.0 mm. long; the buds glabrous. Stamens subequal, exserted to 2.0 mm. beyond the limb, adnate to the corolla tubes equally ca. 3/4 the length from base to limb, the veins below stamen attachments winged (sometimes faintly) near the points of attachment. Styles 4.7–6.0 mm. long, cleft 0.4–0.5 mm. (ca. 1/15–1/9 the length). Nutlets (Figure 9N) 2 or 3, blotched gray and brown, hemi-ovoid, (1.4) 1.7–2.0 mm. tall, 1.0–1.5 mm. across, 0.7–1.0 mm. thick. Cotyledons (after germination) elliptical. Chromosome number, $n = 16$.

DISTRIBUTION: Coastal Peru, in departments of Arequipa, Ica, La Libertad, Lambayeque, Lima, and Piura (Figure 25). *Tiquilia dichotoma* is often found growing in shifting sands, growing alone

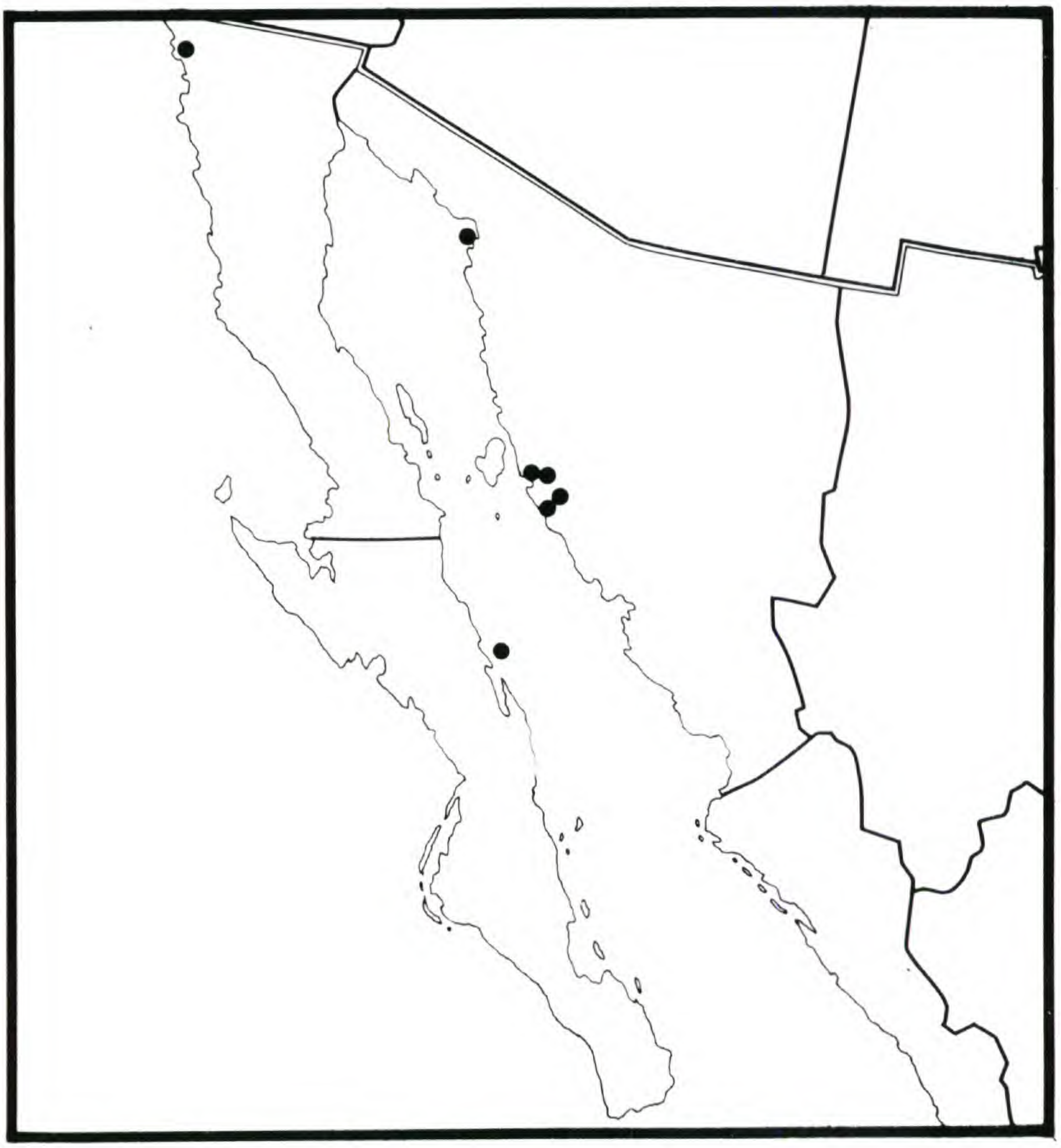

Figure 23. Distribution of *Tiquilia cuspidata*.

or in association with *Alternanthera pubiflora, Baccharis glutinosa, Cristaria multifolia, Galvezia suffruticosa, Grabowskia boerhavifolia,* and *Tribulus terrestris.* It often grows with *T. paronychioides,* and in a population at its southernmost known distribution was found growing with *T. ferreyrae, T. litoralis,* and *T. simulans* as well as *T. paronychioides.* This species is most abundant and most vigorous in northern Peru.

The recorded flowering times are January through June, and August through October.

Tiquilia dichotoma is the type species of the genus. The generic epithet was undoubtedly given in recognition of the vernacular

name, "Tiquil-tiquil," as reported by Ruiz & Pavon (1799), although cited by Persoon (1805) as "Tiquilo."

Two collections vary somewhat from the normal range of morphological characters for the species: *Richardson 2098,* growing with *Tiquilia paronychioides,* and *Richardson 2151A,* growing with *T. ferreyrae, T. litoralis, T. paronychioides,* and *T. simulans.* Since these populations occur in the southern extreme for the species, the slight morphological differences are attributed to environmental effects.

Tiquilia dichotoma is most closely related to *T. simulans.* Johnston (1956) in describing *T. simulans,* suggested the possibility of its being simply a foliar variety of *Tiquilia dichotoma.* Distinguishing and contrasting characters of the two species are listed below.

COMPARISON OF TIQUILIA DICHOTOMA & TIQUILIA SIMULANS

T. dichotoma	*T. simulans*
1. Leaf blades oblong or ovate, 9.0–20.0 mm. long; 3–6 pairs of plicate lateral veins; margins crenate.	1. Leaf blades ovate, 7.5–11.0 mm. long; 2–3 pairs of lateral veins; margins entire.
2. Calyx pubescence more dense along lobe margins.	2. Calyx pubescence more dense apically.
3. Corollas 5.0–6.0 mm. long.	3. Corollas 4.5–5.5 mm. long.
4. Stamens usually subequal.	4. Stamens markedly unequal.
5. Styles 4.7–6.0 mm. long, cleft 1/15–1/9 the length.	5. Styles 4.7–6.0 mm. long, cleft 1/8–1/6 the length.
6. Nutlets hemi-ovoid, the flattened ventral surfaces usually extending the full length and width of the nutlets.	6. Nutlets more or less hemi-ovoid, the flattened ventral surfaces narrowed by inrolling of carpel margins.

15. **Tiquilia simulans** (I. M. Johnston) A. Richardson, Sida **6:** 237. 1976.

Coldenia simulans I. M. Johnston, Jour. Arnold Arb. **37:** 298. 1956. TYPE: **Peru:** AREQUIPA. El Jaguay (sic), km. 538, 22 Aug. 1948, *Scolnik 1010* (Holotype, GH!).

Procumbent or spreading, forming mats or mounds to 12.0 dm. across; caudices to 10.0 mm. thick; older stems woody, bark lurid or sooty colored; young stems with spreading or antrorsely inclined

hairs to 1.0 mm. long. Leaf blades (Figure 7B) green, ovate, 7.5–11.0 mm. long, 3.0–4.0 mm. broad, with 2–3 pairs of lateral veins, the margins entire; upper surfaces with antrorsely closely-appressed hairs to 0.6 mm. long, with few inconspicuous antrorsely appressed bristles to 0.6 mm. long with thickened mineralized bases; lower surfaces with dense antrorsely appressed hairs covering the lateral veins, or less dense and with spreading hairs on the lateral veins; petioles linear, often broader basally, 4.0–5.0 mm. long with spreading hairs to 1.1 mm. long, more dense and longer basally. Flower clusters bracteate. Calyces persistent, ca. 4.5 mm. long, with antrorsely appressed or inclined hairs to 1.0 mm. long, more dense apically; lobes subulate, free ca. 1/2 the length, each with several apical bristles to 0.7 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas lilac to sky-blue or milk-white, 4.5–5.5 mm. long; the buds glabrous. Stamens unequal, exserted to 3.0 mm. beyond the limb, adnate to the corolla tubes subequally ca. 2/3 the length from base to limb, the veins below the stamen attachments with thick wings beginning near the points of insertion, becoming membranous below and tapering toward the base. Styles 4.7–6.0 mm. long, cleft 0.6–1.0 mm. (1/8–1/6 the length). Nutlets (Figure 10A) usually 1 or 2, occasionally 3, rarely 4, blotched gray and brown, more or less hemi-ovoid with the minutely colliculate carpel margins curving slightly around the ventral surfaces, 1.6–2.0 mm. tall, 1.1–1.5 mm. across, 0.6–1.1 mm. thick. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia simulans* is known only from the department of Arequipa, Peru, growing in sands at or near the coast, from Puerto Lomas to the lomas south of Atico (Figure 25). It is most abundant at the coast, growing alone or with *T. litoralis* and *T. paronychioides*. In one population about 15 kilometers inland, it grows intermingled with *T. dichotoma, T. ferreyrae, T. litoralis,* and *T. paronychioides*.

The type locality is "El Jahuay" rather than "El Jaguay" as noted on the holotype. Jaguay is located ca. 183 km. south of Lima in the department of Lima, whereas El Jahuay is located ca. 538 km. south of Lima in the department of Arequipa, agreeing with the kilometer notation on the holotype label.

The recorded flowering times are January, April, May, August, and October.

Tiquilia simulans is most closely related to *T. dichotoma.* Contrasting and distinguishing characters are listed in the discussion of that species.

16. **Tiquilia grandiflora** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia grandiflora Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** Tarapacá. Médanos de Pica, Mar. 1885, *F. Philippi s.n.* (Holotype, SGO 054661! Fragment of holotype, GH! Photograph, NY!).

Procumbent, forming mats to 10.0 dm. across; caudices to 10.0 mm. thick; older stems woody with brown bark; young stems glandular. Leaf blades (Figure 7C) green, narrowly ovate to lanceolate, 11.0–19.0 mm. long, 3.0–5.0 mm. broad, with 3–4 pairs of plicate lateral veins, the margins crenate or entire; upper surfaces with appressed hairs to 0.5 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, or occasionally all hairs antrorsely appressed; lower surfaces with spreading hairs along the veins and margins; petioles filiform, 6.0–10.0 mm. long, glandular and with sparse bristles to 0.5 mm. long, becoming dense basally. Flower clusters bracteate. Calyces persistent, 5.0–8.0 mm. long, glandular with sparse antrorsely inclined hairs to 0.3 mm. long; lobes narrowly triangular, free ca. 1/2 the length, ciliate, the inner surfaces with dense appressed hairs to 0.6 mm. long. Corollas blue to purple or salmon, with cylindrical tubes, 8.5–13.0 mm. long, without appendages; the buds glandular or glabrous. Stamens subequal, well exserted, up to 8.0 mm. beyond the corolla limb, adnate equally to the corolla tubes ca. 5/6 the length from base to limb, the anthers red. Styles 8.5–13.0 mm. long, cleft 0.5–1.0 mm. (1/20–1/10 the length). Nutlets (Figure 10B) 1–4, usually 1 or 2, blotched gray and brown, hemi-ovoid, 2.4–3.2 mm. tall, 1.1–1.5 mm. across, 0.7–0.9 mm. thick, each with a ventral knife-like collar ca. 0.1 mm. broad apically to 0.4 mm. broad basally. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia grandiflora,* although not abundant, has a rather broad north-south distribution from southern Peru in the department of Arequipa to northern Chile, provinces of Antofagasta, Atacama, and Tarapacá (Figure 26), growing in sand principally at medium altitudes of 1800–2400 meters in the inland deserts, but also at the coast. It is not reported growing with any other plant except *T. elongata.*

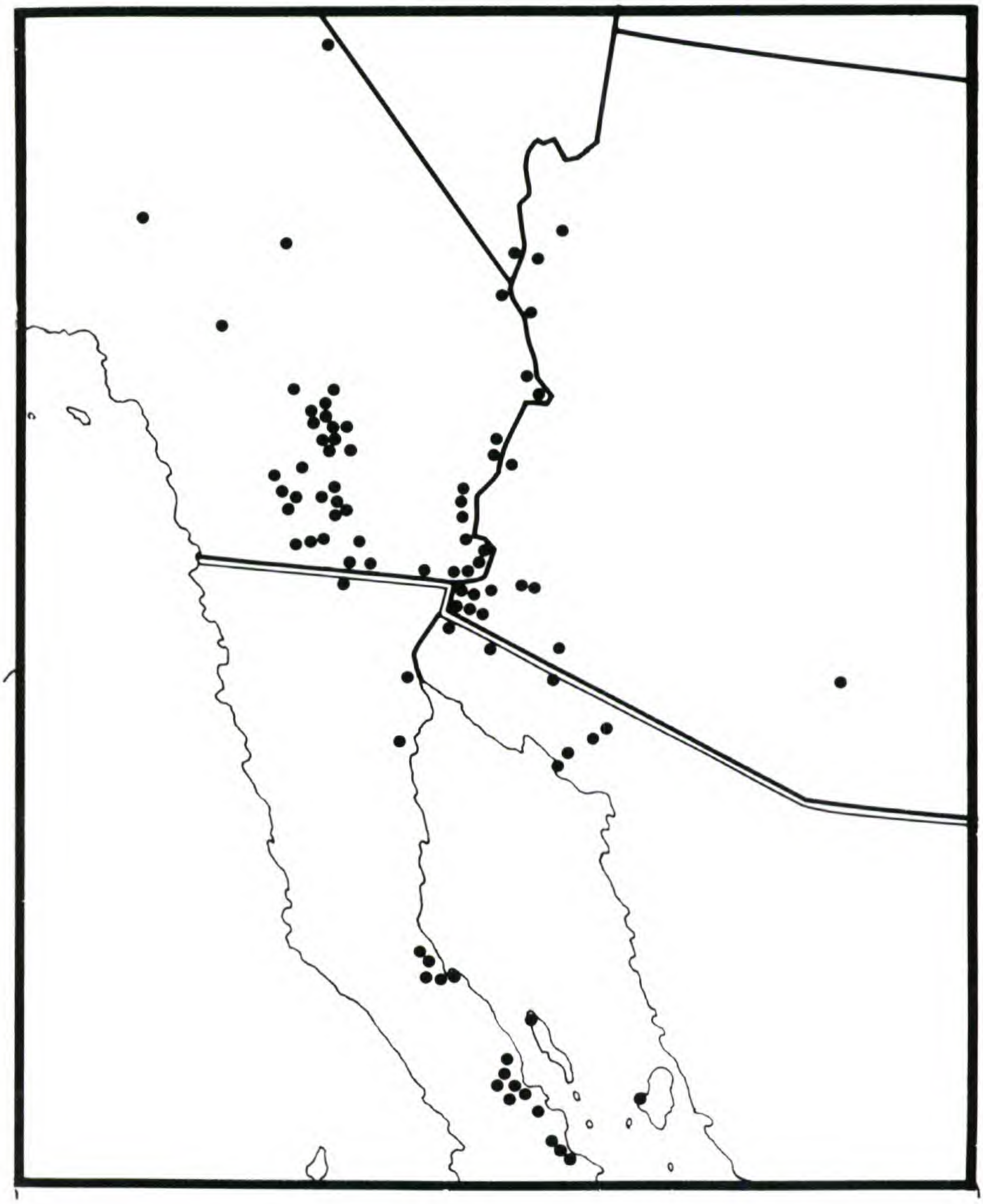

Figure 24. Distribution of *Tiquilia palmeri*.

The recorded flowering times are March, April, October, and November.

Tiquilia grandiflora is most closely related to *T. dichotoma,* but is easily distinguished from that species by its glandular stems and calyces, much larger corollas, and the knife-like ventral collars on the nutlets.

17. **Tiquilia ferreyrae** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia ferreyrae I. M. Johnston, Jour. Arnold Arb. **37:** 296–298. 1956. TYPE: **Peru:** AREQUIPA. In sand along highway between Nazca and Chala, km. 545–546, 7 Nov. 1947, *Ferreyra 2506* (Holotype, A!).

Procumbent, forming mats to 11.0 dm. across; caudices to 10.0 mm. thick; older stems woody with lurid bark; young stems with dense spreading or antrorsely inclined hairs to 0.8 mm. long. Leaf blades (Figure 7D) green to gray, ovate to narrowly ovate, 8.5–11.0 mm. long, 4.0–6.0 mm. broad, with 2–3 (rarely 4) pairs of occasionally plicate lateral veins, the margins entire (rarely crenate); upper surfaces with antrorsely appressed hairs to 0.8 mm. long; lower surfaces with spreading hairs along the veins, sometimes with sparse appressed hairs between the veins; petioles filiform, 4.0–6.0 mm. long with spreading hairs to 0.8 mm. long. Calyces deciduous, 5.0–6.5 mm. long, glandular, with spreading or antrorsely inclined hairs to 0.8 mm. long; the basal portion indurated, thickened, deeply sulcate along the lobe sutures, often retaining the nutlets; lobes narrowly triangular, free ca. 1/2 the length, inner surfaces with sparse appressed hairs apically. Corollas white, rarely lilac color, 7.5–10.0 mm. long, the tubes cylindrical, without appendages. Stamens unequal, well exserted, up to 5.0 mm. beyond the corolla limb, adnate equally to the corolla tubes ca. 4/5 the length from base to limb. Styles 10.0–12.8 mm. long, cleft 0.5–0.8 mm. (1/20–1/15 the length). Nutlets (Figure 10C) 1–4, usually 2, blotched gray, brown, and black, ovoid, 1.4–1.7 mm. tall, 1.1–1.4 mm. across, 1.0–1.1 mm. thick, the flattened ventral surfaces ca. 1.4 mm. tall, 0.8 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia ferreyrae* is known only from the department of Arequipa, Peru, growing in sands at or near the coast in a limited area from ca. 15 km. NE of Puerto Lomas to ca. 15 km. SE of Camaná (Figure 25). It grows regularly with *T. litoralis,*

and in one population was found growing with *T. dichotoma, T. litoralis, T. paronychioides,* and *T. simulans.*

The recorded flowering times are March through May and October through December.

This well-marked species is most closely related to *Tiquilia simulans* and can be easily distinguished from that species by its larger corollas, nutlets with reduced flattened ventral surfaces, and the deciduous indurated sulcate calyces.

Tiquilia sect. **Sphaerocarya** I. M. Johnston, Contr. Gray Herb. **70:** 57. 1924. TYPE: *Tiquilia litoralis* (Phil.) A. Richardson.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades narrowly ovate, ovate, lanceolate, obovate, or narrowly obovate; petioles filiform. Flowers in bracteate clusters with the leaves or solitary at the nodes. Calyces persistent. Corollas deciduous. Stamens included or slightly beyond the corolla limbs, equal or unequal, adnate to the corolla tubes at 3 levels or equally. Style attachments apical, or (*T. conspicua*) gynobasic. Fruits lobed, of 1–4 nutlets. Nutlets spheroid or (*T. atacamensis*) ovate-elliptical, blotched grey, brown, and black, minutely colliculate. Chromosome numbers, $n = 16, 15, \& 14$.

This section includes six species in South America in northern Chile and southern Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. SPHAEROCARYA

a. Nutlet spheroid. ..... b.
b. Leaf margin entire; corolla lilac, sky-blue, or milk-white. ..... c.
c. Corolla 4.5–8.0 mm. long; nutlet without a basal plug from the receptacle; style attachment apical. ..... d.
d. Nutlet with a protruding lip above the attachment scar; stamens exserted, adnate equally to the corolla tube. ..... 19. *T. tacnensis.*
d. Nutlet without a protruding lip above the attachment scar; stamens included or barely exserted, adnate to the corolla tube at three levels. ..... 22. *T. litoralis.*
c. Corolla 7.0–13.5 mm. long; nutlet with a basal plug from the receptacle; style attachment gynobasic. ..... 23. *T. conspicua.*
b. Leaf margin crenate; corolla blue. ..... e.
e. Leaf blade 10.0–23.0 mm. long with 3–4 pairs of lateral veins, upper surface with 2 kinds of hairs; corolla 5.5–12.0 mm. long; longest stamen filament 0.7–1.0 mm. long; nutlet 0.8–0.9 mm. across. ..... 20. *T. elongata.*
e. Leaf blade 5.0–6.0 mm. long with 2–3 pairs of lateral veins, upper surface

with 1 kind of hair; corolla 5.5–6.5 mm. long; longest stamen filament 0.3 mm. long or less; nutlet 0.7–0.8 mm. across. ..... 21. *T. hunteri.*

a. Nutlet ovate in ventral view, elliptical, beaked in lateral view. .....
..... 18. *T. atacamensis.*

18. **Tiquilia atacamensis** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia atacamensis Phil., Florula Atacamensis. 211. 1860. TYPE: **Chile:** ANTOFAGASTA. In sand and gravel near San Pedro de Atacama, Jan. 1854, *R. Philippi s.n.* (Holotype, SGO 054649! Fragment of holotype, GH! Photograph of holotype, NY!).

Coldenia parviflora Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** ANTOFAGASTA. Near Socaire, 2 Feb. 1885, *Fr. Philippi s.n.* (Holotype, SGO 054653! Photograph of holotype, NY! Possible isotypes, GH! SGO 042280!).

Procumbent, forming mats to 6.0 dm. across; caudices to 0.5 cm. thick; older stems woody with whitish to lurid colored bark; young stems with antrorsely appressed or sharply inclined straight hairs to 0.5 mm. long. Leaf blades (Figure 7E) gray-green, narrowly ovate to ovate, 5.0–8.0 mm. long, 2.0–4.0 mm. broad, with 2 pairs of plicate lateral veins, the margins entire; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely inclined or appressed marginally, also with occasional inclined bristles to 0.5 mm. long and 1 or 2 apical bristles to 0.5 mm. long; lower surfaces with appressed and spreading hairs to 0.3 mm. long (leaves on specimens from Pica are larger and have many stiff antrorsely inclined bristles to 0.9 mm. long); petioles expanding near the base, 4.0–7.0 mm. long with spreading hairs to 1.0 mm. long. Calyces 3.5–4.5 mm. long with antrorsely inclined stiff hairs to 0.7 mm. long, more dense along the lobe margins; lobes narrowly triangular, free ca. 1/2 the length, each with 1 or 2 slightly thicker apical hairs to 0.5 mm. long, the inner surfaces with sparse antrorsely appressed hairs. Corollas violet to lilac with yellow to orange throats, the color fading with age, 4.0–5.5 mm. long; the buds villulose and glandular. Stamens unequal, slightly exserted, adnate to the corolla tubes at 3 levels ca. 1/2 the length from base to limb, the veins below the stamen attachments usually winged near the bases. Styles 2.5–5.0 mm. long, cleft 1/6–1/4 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10D) 4, occasionally less, ovate ventrally, elliptical and beaked laterally, 1.1–1.3 mm. tall, 0.7–1.1 mm. across. Chromosome number not known.

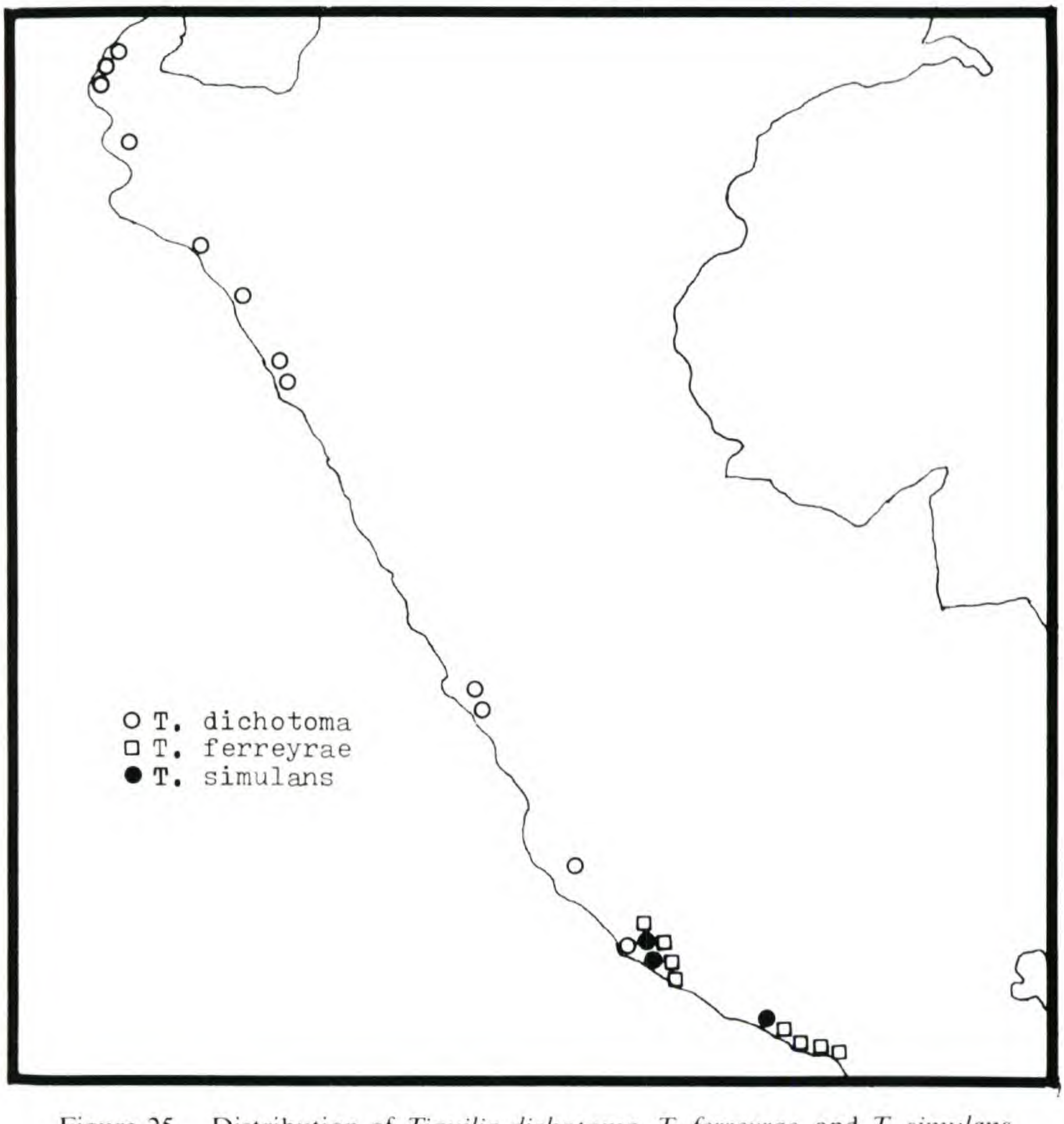

Figure 25. Distribution of *Tiquilia dichotoma*, *T. ferreyrae*, and *T. simulans*.

DISTRIBUTION: Chile, in the provinces of Antofagasta and Tarapacá (Figure 26), mainly in the higher altitude inland deserts at 1400–4100 meters, in sand and gravel. *Tiquilia atacamensis* often grows alone, and is the dominant plant where it occurs. It is extremely abundant near San Pedro de Atacama where large populations covering the hillsides extend for many kilometers. *T. paronychioides* and *Tribulus sp.* sometimes grow in association with this species.

Recorded flowering times are January, February, May, September, and October. More extensive collection of this species would probably reveal a more extended blooming season.

Tiquilia atacamensis is distinct from all other species in the sect. *Sphaerocarya* in having ovate-elliptical, beaked nutlets rather than spheroid nutlets. It is most closely related to *T. tacnensis,* which has similar calyces and general pubescence and a similar flavonoid chromatograph pattern (Richardson, 1975, unpublished). The two species are contrasted below.

COMPARISON OF TIQUILIA ATACAMENSIS & TIQUILIA TACNENSIS

T. atacamensis	*T. tacnensis*
1. Internodes usually thick and short.	1. Internodes usually slender and elongate.
2. Leaves 5.0–8.0 mm. long, 2 pairs of lateral veins.	2. Leaves 4.0–5.5 mm. long, usually 3 pairs of lateral veins.
3. Corollas violet to lilac, appendaged.	3. Corollas sky blue, not appendaged.
4. Stamens slightly exserted.	4. Stamens exserted 1.5–2.5 mm.
5. Nutlets ovate-elliptical, beaked, with smaller collicula.	5. Nutlets spheroid, not beaked, with an apical lip, with larger collicula.

19. **Tiquilia tacnensis** A. Richardson, Sida **6:** 238–240. 1976. TYPE: **Peru:** Tacna. Ca. 10 km. S of Camiara, 70 km. N of Tacna, 13 Apr. 1973, *Richardson 2130* (Holotype, TEX! Isotypes, ARIZ! CAS! F! GH! MICH! NY! POM! UC! US!).

Procumbent, forming mats to 5.0 dm. across; caudices to 10.0 mm. thick; older stems woody with sooty colored bark; young stems with antrorsely appressed or inclined straight hairs to 0.5 mm. long. Leaf blades (Figure 7F) olive green, ovate, 4.5–5.5 mm. long, 3.0–3.5 mm. broad, with usually 3 pairs (occasionally 2 pairs) of plicate lateral veins, the margins entire; upper surfaces with appressed hairs to 0.3 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely appressed marginally, also with occasional inclined bristles to 0.7 mm. long; lower surfaces with dense spreading and appressed straight hairs to 0.5 mm. long, often covering all but the midvein; petioles 3.0–4.0 mm. long with dense antrorsely inclined hairs to 0.8 mm. long. Calyces ca. 3.5 mm. long with antrorsely inclined

stiff hairs to 1.0 mm. long, more dense along the margins; lobes narrowly triangular, free ca. 1/2 the length, each with 1 or 2 slightly thicker apical hairs to 0.5 mm. long, the inner surfaces with sparse appressed hairs. Corollas sky blue with yellow throats, 5.0–6.0 mm. long; the buds glandular. Stamens subequal, exserted 1.5–2.5 mm. beyond the limb, adnate to the corolla tubes equally ca. 1/2 the length from base to limb, the veins below stamen attachments not appendaged. Styles 5.5–5.6 mm. long, cleft 1/9–1/5 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10E) 4, occasionally less, colliculate, spheroid with a protruding lip above the attachment scar, 1.0–1.1 mm. tall, 0.9–1.2 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: Peru, southern Tacna near the Chilean border (Figure 27). One large uniform population is known. Extending for ca. 30 kilometers, it is the dominant plant growing in sand with *Argelia feullei, Nolana sp.*, and various grasses.

This species is known to flower in November and April.

The specific epithet was given in recognition of the department of Tacna, Peru, to which the species is endemic.

Tiquilia tacnensis appears to be most closely related to *T. atacamensis*, having a similar flavonoid chromatograph pattern (Richardson, 1975, unpublished), and similar calyces and general pubescence. The two species are contrasted in the discussion of *T. atacamensis*.

Tiquilia tacnensis is also closely related to *T. litoralis*, differing in flavonoid chromatograph pattern, chromosome number of $n = 16$, leaf blades with usually 3 pairs of lateral veins, paucity or absence of long stiff bristles on the calyces, and the nutlets with a protruding lip above the attachment scar and with slightly larger collicula. There are also some similarities to *T. elongata* and *T. hunteri*.

20. **Tiquilia elongata** (Rusby) A. Richardson, Sida **6:** 236. 1976.

Coldenia elongata Rusby, Description of Three Hundred New Species of South American Plants. Rusby. New York. p. 107. 1920. TYPE: **Peru:** AREQUIPA. Dry hillsides, Yura, 10 Aug. 1901, *Williams 2562* (Holotype, NY! Isotype, NY! Fragment and photograph of isotype, GH!).

Procumbent or semi-erect subshrubs forming mounds to 1 meter across; caudices to 10.0 mm. thick; older stems with light brown or

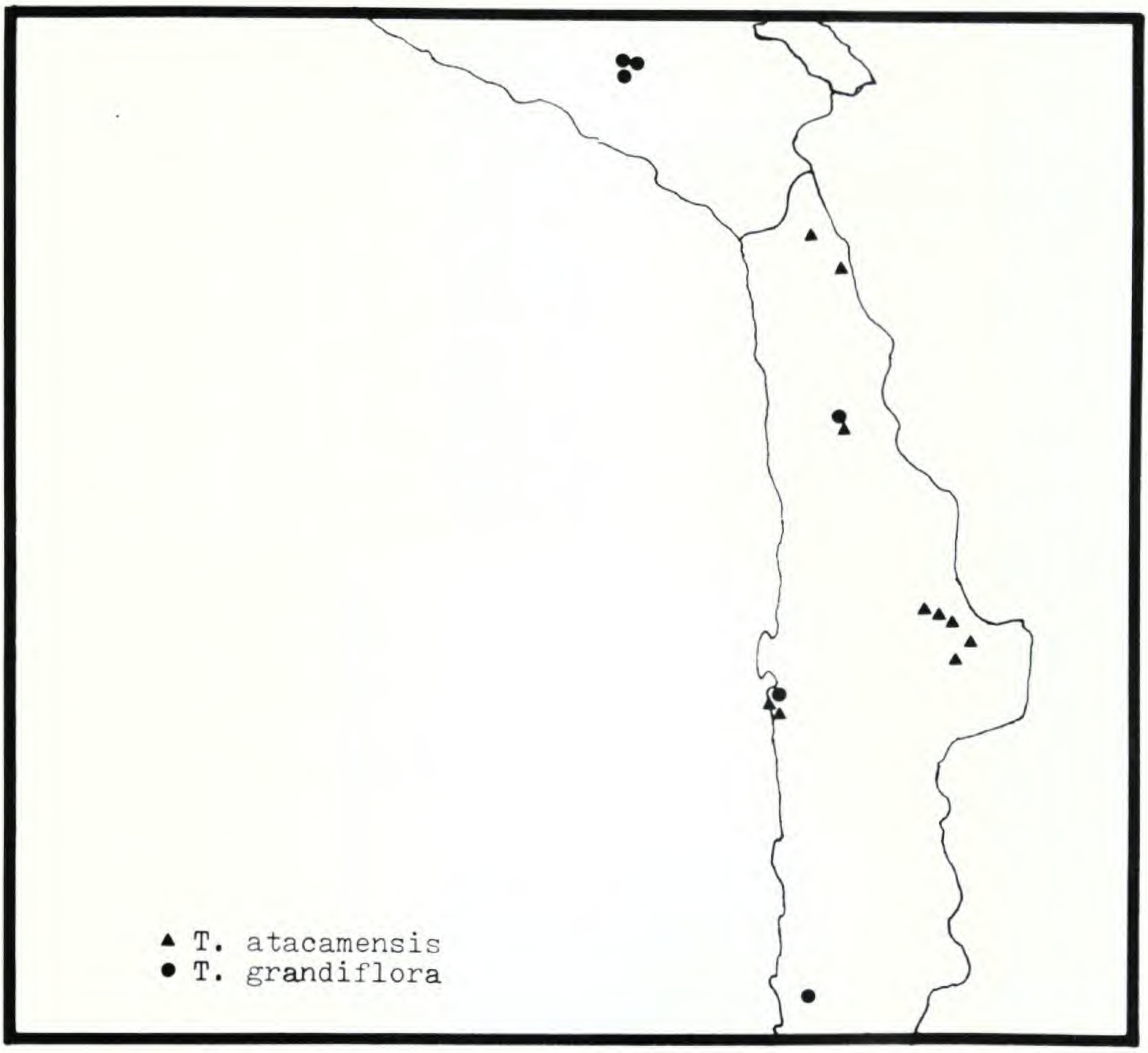

Figure 26. Distribution of *Tiquilia atacamensis* and *T. grandiflora.*

whitish bark; young stems with dense spreading or antrorsely inclined straight hairs to 1.2 mm. long, sometimes hoary. Leaf blades (Figure 7G) narrowly ovate to lanceolate or narrowly obovate, 10.0–23.0 mm. long, 3.0–10.0 mm. broad, the margins crenate, 3–4 pairs of usually plicate lateral veins running to the sinuses; upper surfaces with antrorsely appressed or inclined hairs to 0.4 mm. long and scattered thicker hairs to 0.9 mm. long with thickened mineralized bases; lower surfaces with dense spreading hairs especially along the veins; petioles 6.0–16.0 mm. long with dense spreading hairs to 1.0 mm. long. Calyces 4.0–5.5 mm. long with antrorsely inclined stiff hairs to 1.5 mm. long; lobes linear to narrowly triangular, free ca. 4/5 the length, each with 1 or few apical bristles to 0.7 mm. long, ciliate with hairs to 0.8 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas blue, sometimes

constricted at the throat, 5.5–12.0 mm. long; the buds villulose. Stamens unequal, included; filaments to 1.0 mm. long, adnate to the corolla tubes at 3 levels ca. 3/7 the length from base to limb, the veins below the stamen attachments usually winged. Styles 4.0–6.2 mm. long, cleft 1/5–1/4 the length, attached to the nutlets apically. Nutlets (Figure 10F) 4, sometimes less, spheroid, 0.8–0.9 mm. across. Chromosome number, $n = 16$.

DISTRIBUTION: *Tiquilia elongata* is limited almost entirely to the inland desert in southern Peru, department of Arequipa, growing in sand, sandy clay, and volcanic ash (Figure 28). It is most abundant around Arequipa and Yura. One collection (*Richardson 2129*) was made from a few plants growing near the coast in Peru's southernmost department, Tacna. This species is usually dominant where it occurs, growing alone or with species of *Encelia, Franseria,* and various cacti. It grows with *T. grandiflora* and *T. paronychioides.*

Flowering seasons are January through April, June through August, October, and November.

A vernacular name for this plant is "Paco-paco."

Tiquilia elongata is easily distinguished from the other species of sect. *Sphaerocarya* that have apical styles and spheroid nutlets by its blue corollas and large crenate leaves with two kinds of hairs on the upper surface. It is also fairly well separated geographically from these species.

21. **Tiquilia hunteri** A. Richardson, Sida **6:** 238, 239. 1976. TYPE: **Peru:** AREQUIPA. Km. 714 S of Lima, between Chala and Camaná, 8 Apr. 1973, *Richardson 2106* (Holotype, TEX! Isotypes, CAS! F! GH! UC! US!).

Semi-erect subshrubs with internodes to 2.0 cm. long, forming mounds to 4.0 dm. across; caudices to 5.0 mm. thick; older stems with whitish bark; young stems with dense spreading hairs to 1.5 mm. long. Leaf blades (Figure 7H) green, narrowly ovate, 5.0–6.0 mm. long, 2.0–2.5 mm. broad, the margins usually crenate, sometimes entire, 2–3 (rarely 4) pairs of deeply plicate lateral veins running to the sinuses; upper surfaces with antrorsely inclined thick white bristles to 1.1 mm. long with thickened mineralized bases, each blade with a stout apical bristle; lower surfaces with spreading hairs mostly along the veins; petioles 3.0–4.5 mm. long with

spreading hairs to 1.2 mm. long. Calyces ca. 4.0 mm. long with sparse antrorsely inclined hairs to 0.5 mm. long; lobes narrowly triangular, free ca. 3/4 the length, ciliate, each with a stiff apical bristle to 0.8 mm. long, inner surfaces with sparse antrorsely appressed hairs. Corollas blue, sometimes constricted at the throat, 5.5–6.5 mm. long; the buds glandular. Stamens unequal, included, filaments short, to 0.3 mm. long, adnate to the corolla tubes at 3 levels ca. 3/5 the length from base to limb, the veins below stamen attachments lightly winged basally. Styles 4.0–4.5 mm. long, cleft ca. 1/9 the length, exserted beyond the calyces; attached to the nutlets apically. Nutlets (Figure 10G) 4, occasionally less, spheroid, 0.7–0.8 mm. across. Chromosome number, $n = 14$.

DISTRIBUTION: Known only from the type locality (Figure 27). One small, uniform population is known, growing in roadside sands with *Tiquilia litoralis*.

The specific epithet was given in recognition of my friend John H. Hunter (born 1900) of Brownsville, Texas, who has encouraged and aided many students interested in the biological sciences.

Tiquilia hunteri is most closely related to *T. elongata,* from which it is well separated geographically. It is also closely related to *T. litoralis* and *T. tacnensis*.

22. **Tiquilia litoralis** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia litoralis Phil., Florula Atacamensis. 211. 1860. TYPE: **Chile:** ATACAMA. In littoral sand at Caldera, Dec. 1853, *Philippi s.n.* (Holotype, SGO 042286! Possible isotypes, SGO 054659! GH! Photographs of holotype, GH! NY!).

Coldenia mitis Phil., Anales Univ. Chile **90:** 229. 1895. TYPE: **Chile:** ATACAMA. Desert of Atacama, Quebrada del Rosario, *San Roman s.n.* (Holotype, SGO 054654! Photograph of holotype, NY!).

Coldenia virens Phil., Anales Univ. Chile **90:** 229, 230. 1895. TYPE: **Chile:** ATACAMA. Near Caldera, Sep. 1885, *Philippi s.n.* (Holotype, SGO 054658!).

Procumbent with elongate internodes to 5.0 cm. long, forming mats to 6.0 dm. across; caudices to 10.0 mm. thick; older stems woody with whitish bark; young stems with dense spreading hairs to 1.0 mm. long. Leaf blades (Figure 7I) green to olive-green, ovate, 3.5–8.0 mm. long, 2.5–4.5 mm. broad, with 2–3 pairs of often plicate lateral veins, the margins entire; upper surfaces with inclined or appressed hairs to 0.5 mm. long converging on the medians between the veins and flowing toward the margins, antrorsely inclined or appressed marginally, and with scattered an-

trorsely inclined thick bristles to 1.0 mm. long with thickened mineralized bases (sometimes all hairs antrorsely inclined or appressed); lower surfaces with spreading hairs to 0.8 mm. long, mainly along the veins; petioles 4.0–8.0 mm. long with dense spreading hairs to 1.0 mm. long. Calyces 4.5–5.0 mm. long with antrorsely inclined bristles to 1.0 mm. long; lobes narrowly triangular, free ca. 3/5 the length, each with 1 or 2 apical bristles to 1.0 mm. long, inner surfaces with sparse appressed hairs. Corollas sky-blue to milk-white with yellow throats, 4.5–8.0 mm. long; the buds villulose. Stamens unequal, reaching the limb, the longest ones occasionally slightly exserted; filaments to 17.0 mm. long, adnate to the corolla tubes at 3 levels ca. 3/5 the length from base to limb, the veins below the stamen attachments lightly winged near the bases or without appendages. Styles 3.0–6.3 mm. long, cleft 1/5–1/3 the length, exserted beyond the calyces, attached to the nutlets apically. Nutlets (Figure 10H) 4, occasionally less, spheroid, 0.8–1.1 mm. across. Chromosome number, $n = 15$.

DISTRIBUTION: Chile, in the provinces of Antofagasta, Atacama, and Tarapacá; and Peru, in the departments of Arequipa and Tacna (Figure 28). *Tiquilia litoralis* is almost entirely limited to the littoral sands of these countries and is usually the dominant plant. It grows alone or in association with *Perityle emoryi* and species of *Frankenia, Nolana,* and *Onoseris.* It often grows with *T. ferreyrae* and is occasionally found growing with *T. paronychioides* and *T. simulans.*

Tiquilia litoralis flowers January through May, and August through December.

One specimen, *Richardson 2149,* is difficult to place, having the included stamens and spheroidal nutlets of sect. *Sphaerocarya,* and the persistent corolla, flattened but reduced ventral nutlet surface, and chromatographic profile of *T. simulans* of sect. *Tiquilia.* This collection was made from a single plant growing in a large mixed population of *T. simulans* (*Richardson 2150*) and *T. litoralis* (*Richardson 2151*). Corolla color, plant habit, and vegetative morphology were almost identical to those of the surrounding plants of *T. simulans.* A careful search revealed no additional similar plants, but they could have been overlooked since there were many plants without flowers. In the absence of populational data, this specimen is referred to *T. litoralis.*

Tiquilia litoralis, T. tacnensis, T. elongata, and *T. hunteri* are closely related and have morphological similarities that sometimes make them difficult to distinguish without close examination.

23. **Tiquilia conspicua** (I. M. Johnston) A. Richardson, Sida **6:** 236. 1976.

Coldenia conspicua I. M. Johnston, Jour. Arnold Arb. **16:** 183–185. 1935. TYPE: **Peru:** AREQUIPA. Sand flat at Mejía, 26 Oct. 1923, *Guenther & Buchtien 155* (Holotype, HBG!).

Procumbent, forming mats to 5.0 dm. across, dichotomous branching not conspicuous; caudices to 6.0 mm. thick; older stems somewhat woody, bark sooty colored; young stems with spreading or inclined hairs 1.1–1.5 mm. long. Leaf blades (Figure 8A) green, ovate to elliptical, 7.0–12.0 mm. long, 3.0–5.5 mm. broad, with 2 pairs of lateral veins, the margins narrowly revolute, entire; upper surfaces with antrorsely inclined straight hairs to 1.0 mm. long and thicker bristles to 1.2 mm. long with mineralized bases; lower surfaces with spreading hairs to 1.0 mm. long, especially along margins and veins; petioles 4.5–11.0 mm. long with dense spreading hairs to 1.3 mm. long. Calyces 6.5–10.0 mm. long with spreading and antrorsely inclined hairs 1.0–1.5 mm. long, especially along the lobe margins; lobes narrowly triangular, free nearly to the base, each lobe with 2 or several bristles to 1.0 mm. long at or near the apex, inner surfaces with sparse appressed hairs. Corollas lilac color, 7.0–13.5 mm. long; the buds glandular. Stamens subequal, reaching the limb or barely exserted, adnate to the corolla tubes at 3 levels ca. 7/9 the length from base to limb, the veins below the stamen attachments unilaterally winged from about the middle of the tube, tapering near the base. Styles 5.5–9.3 mm. long, cleft ca. 1/6 the length, exserted beyond the calyces; attached basally to a gynobase. Nutlets (Figure 10I) 4, spheroid, 1.0–1.5 mm. across, each nutlet with a basal plug, leaving a cupulate gynobase when falling away. Chromosome number, $n = 16$.

DISTRIBUTION: Peru, in the department of Arequipa, growing in sands mainly along the coast but also at the higher altitudes of Estación Cachendo and Yura (Figure 27). This species has not been reported to be growing with any other plants.

Reported flowering times are April, August, October, and November. More extensive collecting would probably reveal a longer blooming period.

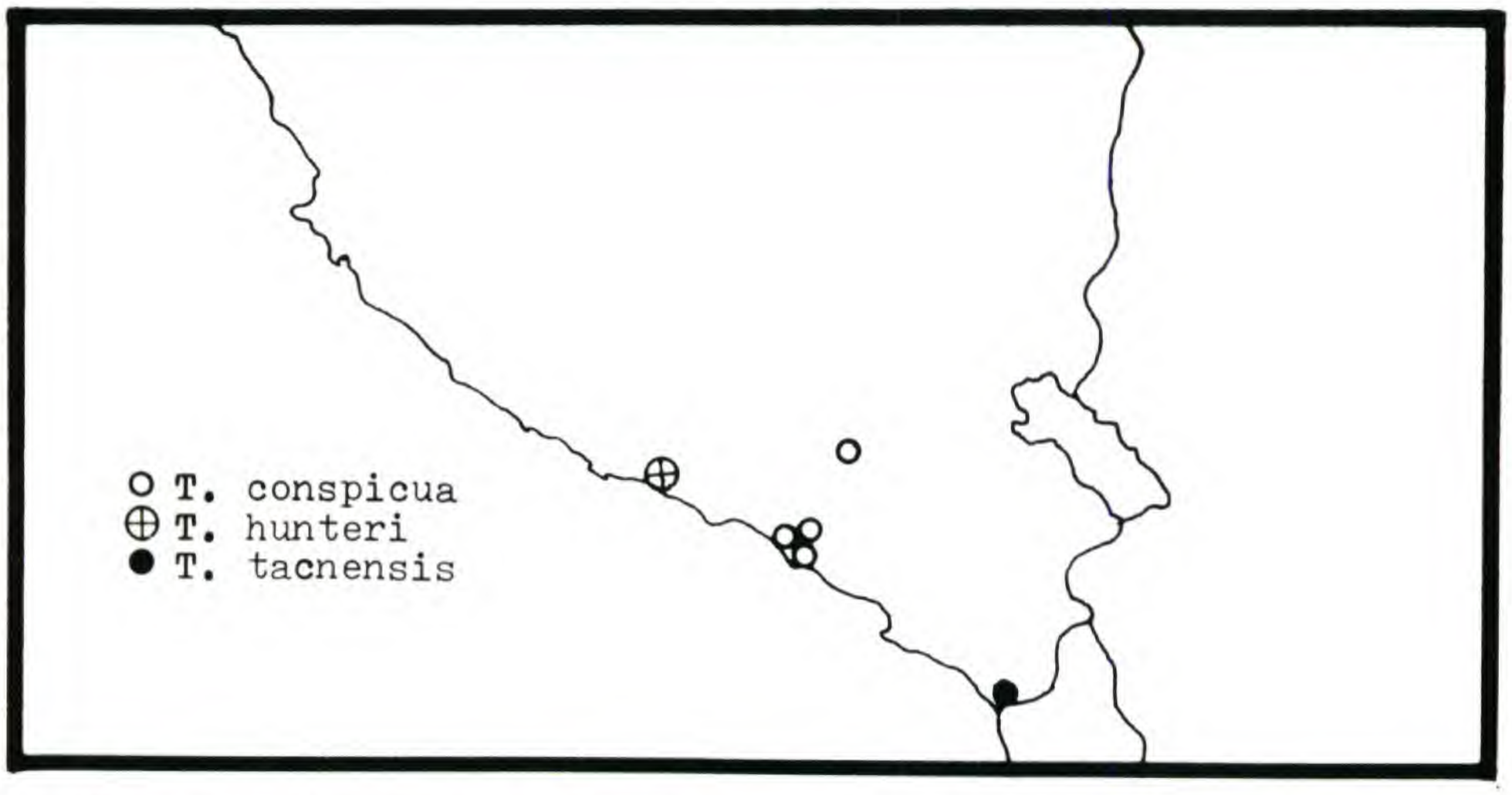

Figure 27. Distribution of *Tiquilia conspicua, T. hunteri,* and *T. tacnensis.*

Tiquilia conspicua differs from other species of the sect. *Sphaerocarya* in having much larger floral parts and nutlets, in its narrowly revolute leaf margins, and its gynobasic style.

One collection, *Mexia 4178,* is in question. This collection consists entirely of small seedlings with flowers but without mature nutlets. The floral parts are much smaller than those of the mature plants examined, but the leaf characters and collection locality fit *Tiquilia conspicua.* Therefore it is referred to this species.

Tiquilia sect. **Galapagoa** A. Richardson. TYPE: *Tiquilia darwinii* (Hooker f.) A. Richardson.

Procumbent or semi-erect, herbaceous to suffrutescent, forming mats or mounds. Leaves solitary at the nodes or in clusters on short branches or stem apices; blades ovate to elliptical, lanceolate, obovate, or narrowly obovate; on plants which have been subjected to long dry periods, blades tend to recurve, giving a convex upper surface and a narrowly ovate to obovate shape; petioles ovate-trullate. Flowers solitary and axillary, or in clusters with the leaves. Calyces deciduous or persistent. Corollas deciduous. Stamens included or slightly beyond the corolla limbs, equal or unequal, adnate to the corolla tubes equally or at 3 levels. Fruits lobed, of 4 nutlets. Nutlets ovoid, black, smooth, granular, or minutely colliculate.

This section includes four species in South America, three of them endemic to the Galapagos Islands, and one widespread species in Chile, Ecuador, and Peru.

KEY TO THE SPECIES OF TIQUILIA SECT. GALAPAGOA

a. Nutlet granular or minutely colliculate, dull. ..... b.
b. Nutlet 0.7–1.2 mm. tall, attachment scar width constant the full length; calyx lobes narrowly triangular. ..... 24. *T. paronychioides.*
b. Nutlet 0.6–1.0 mm. tall, attachment scar widening at apex and base; calyx lobes narrowly ovate. ..... 25. *T. galapagoa.*
a. Nutlet smooth, shiny. ..... c.
c. Nutlet deeper dorsi-ventrally than broad; leaf blade 2.3–4.0 mm. long, lower surface with spreading and antrorsely inclined and appressed hairs along the midrib; corolla 2.5–3.0 mm. long, without appendages; stamens included. ..... 26. *T. nesiotica.*
c. Nutlet more or less the same dimension dorsi-ventrally as broad; leaf blade 2.0–2.7 mm. long, lower surface with antrorsely appressed hairs, none spreading or pointing away from the apex; corolla 1.3–1.7 mm. long with small, unialate wings below the stamen attachments; stamens extending to limb or slightly beyond. ..... 27. *T. darwinii.*

24. **Tiquilia paronychioides** (Phil.) A. Richardson, Sida **6:** 236. 1976.

Coldenia paronychioides Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Pampa Tamarugal, Mar. 1884, *F. Philippi s.n.* (Holotype, SGO 054652! Fragment of holotype, GH! Probable isotype, SGO 042277!).

Coldenia tenuis Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Tambillo Chico, Mar. 1885, *Rahmer s.n.* (Holotype, SGO 042279! Fragment of holotype, GH! Probable isotype, US! Photograph of US probable isotype, NY!).

Coldenia aggregata Rusby, Description of Three Hundred New Species of South American Plants. Rusby. New York. pp. 106, 107. 1920. TYPE: **Peru:** PIURA. Paita, 25 Jul. 1901, *Williams 2913* (Holotype, NY! Fragment of holotype, GH!).

Procumbent, occasionally semi-erect, forming mats to 21.0 dm. across; caudices to 10.0 mm. thick; older stems woody with brown bark; young stems with dense appressed or antrorsely inclined hairs to 0.8 mm. long. Leaf blades (Figure 8B) green to gray-green, narrowly obovate to lanceolate or obovate, 3.0–6.0 mm. long, 1.2–3.0 mm. broad, marginally entire; upper surfaces with antrorsely appressed hairs to 0.3 mm. long, and sparse or dense antrorsely inclined bristles to 1.0 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces with spreading hairs to 0.3 mm. long along the prominent midrib; petioles trullate, sometimes filiform distally,

0.5–5.0 mm. long with dense spreading hairs to 0.8 mm. long. Flowers axillary and solitary, and in ebracteate clusters with the leaves. Calyces deciduous, 2.5–3.5 mm. long with antrorsely inclined or appressed hairs to 1.0 mm. long; lobes narrowly triangular, free 1/3–1/2 the length, ciliate. Corollas white to milk-white, 1.7–4.0 mm. long, the tubes usually cylindrical, without appendages; the buds glabrous. Stamens unequal, included, adnate to the corolla tubes at 3 levels 1/3–1/2 the length from base to limb. Styles 0.7–2.0 mm. long, cleft 1/5–1/3 the length (0.2–0.9 mm.), attached apically or sub-apically to the nutlets. Nutlets (Figure 10J) black, granular, usually unequal in size within a fruit, 0.7–1.2 mm. tall, 0.4–0.7 mm. broad; the attachment scars to 0.2 mm. broad, ca. 0.9 mm. long, not enlarged apically or basally. Cotyledons (after germination) elliptical. Chromosome number, not known.

DISTRIBUTION: *Tiquilia paronychioides* is mainly coastal, from central Ecuador through Peru to northern Chile, occurring also inland around Arequipa, Peru, and in Chile (Figure 29). One collection was made in La Paz, Bolivia, and one in Panama. This species grows in sand or sandy clay in association with *Alternanthera pubiflora, Baccharis glutinosa, Cristaria multiflora, Galvezia suffruticosa, Tribulus terrestris,* species of *Cordia* and *Ipomea,* and various cacti and grasses. It grows with *T. atacamensis, T. dichotoma, T. elongata, T. ferreyrae, T. litoralis,* and *T. simulans,* and is the only species of *Tiquilia* in South America which successfully competes to any degree with other plants.

This species flowers January through December.

Tiquilia paronychioides is known as "flor de arena" and "yerba blanca." It is sometimes used to treat gonorrhea (*Stork, et al. 9197,* GH).

Tiquilia paronychioides varies in leaf morphology. In seedlings, the margins are often not revolute; in older plants which have been receiving copious amounts of water, the blades are often proportionately broader with only slightly revolute margins, and less densely pubescent. The number of bristles present is extremely variable, but fairly consistent within a given population.

In northern Peru and Ecuador, which receive greater amounts of rain than regions farther south, plants are often found with proportionately larger leaves and stems.

There are no closely related species on the mainland of South

America. *Tiquilia paronychioides* is distinct with its smaller leaves and corollas and its smaller, black, ovoid nutlets lacking a broad ventral surface. The species of the Galapagos Islands are the most closely related taxa.

25. **Tiquilia galapagoa** (J. T. Howell) A. Richardson, comb. nov.

Coldenia galapagoa J. T. Howell, Proc. Calif. Acad IV. **12:** 108, 109. 1937. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Conway Bay, Indefatigable Island, 8 Jun. 1932, *Howell 9862* CAS! (Isotypes, CAS! GH!).

Prostrate or somewhat ascending, cinereous, forming mats to 8.0 dm. across; caudices to 10.0 mm. thick; older stems woody with whitish bark; young stems with dense antrorsely appressed and inclined or spreading hairs to 0.7 mm. long. Leaf blades (Figure 8C) suborbicular to ovate or lanceolate, 2.0–5.0 mm. long, 1.5–3.5 mm. broad, marginally entire; upper surfaces with antrorsely appressed or inclined hairs to 0.9 mm. long with thickened mineralized bases, midrib plicate, lateral veins moderately so or indistinct; lower surfaces with spreading hairs along the midribs and lateral veins, or completely covered with antrorsely and marginally appressed hairs; petioles trullate to rectangular, 1.0–2.5 mm. long, ciliate, the abaxial surface with antrorsely appressed hairs or occasionally glabrate. Flowers axillary and solitary, also in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.5–2.5 mm. long, with dense antrorsely inclined hairs to 1.0 mm. long, becoming less dense apically; lobes 5, subequal, narrowly ovate, free ca. 1/2 the length, usually spreading at maturity; the fused bases with 4 cups enclosing the nutlets. Corollas whitish or white with purple, 1.1–2.8 (3.5) mm. long, without appendages; the buds villous. Stamens subequal, included, adnate equally to the corolla tubes ca. 1/3 the length from base to limb. Styles 1.0–2.3 mm. long, cleft 0.7–2.1 mm. or to the base, attached apically to the nutlets. Nutlets (Figure 10K) brown or black, dull, minutely colliculate, 0.6–1.0 mm. tall, 0.4–0.5 mm. broad, the attachment scar nearly the full length, enlarging slightly apically and basally. Cotyledons (after germination) elliptical. Chromosome number, not known.

DISTRIBUTION: Galapagos Islands, in sand at or near the coast, in association with *Bursera* and *Opuntia*. *Tiquilia galapagoa* is the only species of *Tiquilia* growing on Barrington, Brattle, Daphne,

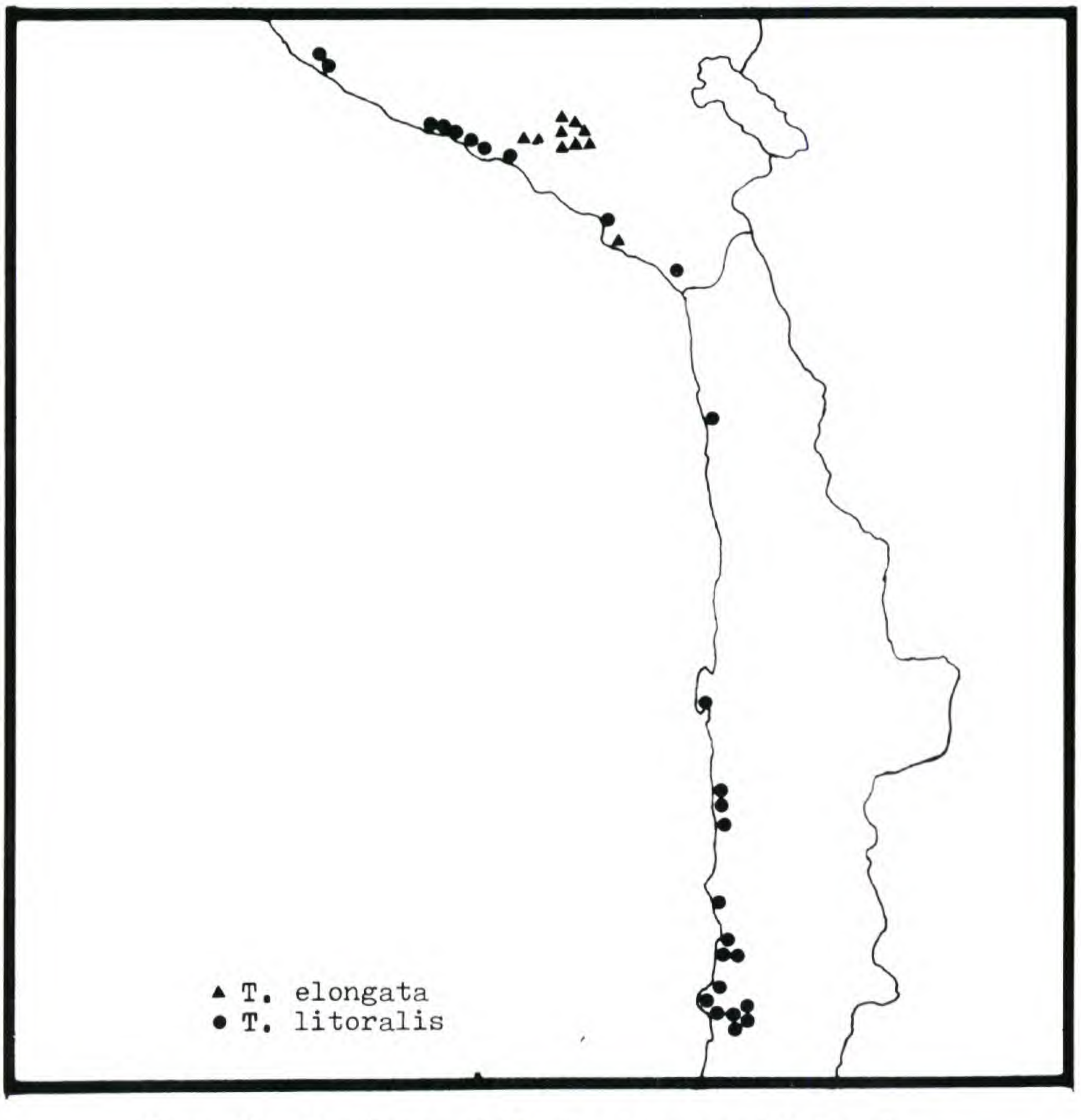

Figure 28. Distribution of *Tiquilia elongata* and *T. litoralis*.

Hood, Indefatigable, Jervis, and South Seymour Islands. It grows on Albemarle and Chatham Islands where *T. darwinii* also occurs, the two species sometimes growing together, and on James Island where *T. darwinii* and *T. nesiotica* are also found.

This species flowers January through December.

Tiquilia galapagoa resembles *T. paronychioides* in its granular nutlets, but differs from that species in its smaller leaves and corollas; its stamens being adnate equally to the corolla tube; its more deeply cleft styles; and its nutlets with narrower attachment scars broadening apically and basally. It is the only Galapagoan species with dull, granular nutlets, the other species having nutlets which are smooth and shiny.

Because of confusion in typification, this taxon has been known as *Coldenia fusca* (Howell, 1937; Wiggins & Porter, 1971). Thanks to recent research by Duncan Porter, who called this investigator's attention to the correct types of *Galapagoa darwinii* and *G. fusca,* this problem can be resolved (See also Porter, 1977).

Examination of the types of *Galapagoa darwinii* and *G. fusca* shows clearly that they are the same. An annotation by J. T. Howell on the holotype of *G. fusca* states that it corresponds with *G. darwinii.* Since *G. darwinii* is the first described, *G. fusca* is a synonym of that taxon; therefore another name is needed for the taxon previously known as *G. fusca.* Using the types designated by Howell (1937), this author had called *Coldenia galapagoa* J. T. Howell a synonym of *Galapagoa fusca,* since it represented a slight variation, with characters which intergraded with *G. fusca.* With *G. fusca* now a synonym of *G. darwinii,* the remaining available name is *Coldenia galapagoa.*

26. **Tiquilia nesiotica** (J. T. Howell) A. Richardson, Sida **6:** 236. 1976.

Coldenia conspicua J. T. Howell, Proc. Calif. Acad. IV. **12:** 105, 106. 1937. TYPE: **Ecuador:** GALAPAGOS ISLANDS. NW side of Bartholomew Island, 14 June 1932, *Howell 10059* (Holotype, CAS! Isotypes, CAS! F! GH! NY! US!). Not *C. conspicua* I. M. Johnston, 1935.

Coldenia nesiotica J. T. Howell, Proc. Calif. Acad. IV. **22:** 237. 1941. *Nom. nov.* based on *Coldenia conspicua* J. T. Howell.

Low spreading or suberect cinereous bushes 3.0–4.0 dm. tall; caudices to 7.0 mm. thick; older stems woody with brown bark; young stems with retrorsely and antrorsely appressed or spreading hairs to 0.4 mm. long. Leaf blades (Figure 8D) ovate-acute, 2.3–4.0 mm. long, 1.0–2.3 mm. broad, marginally entire; upper surfaces with antrorsely appressed hairs to 0.5 mm. long and sparse antrorsely inclined bristles to 7.0 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces with spreading and antrorsely inclined and appressed hairs along the prominent midrib; petioles trullate to ovate, sometimes filiform distally, 1.0–2.8 mm. long, densely ciliate, the abaxial surfaces with dense antrorsely appressed hairs, becoming sparsely pubescent or glabrate. Flowers solitary and axillary, or in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.5–2.0 mm. long, with dense spreading and antrorsely inclined hairs to 0.4 mm. long, and bristles to 0.7 mm. long apically; lobes 5, equal, subulate, free ca. 1/2 the

length. Corollas white, 2.5–3.0 mm. long, without appendages; the buds villous. Stamens included, unequal, adnate equally to the corolla tubes ca. 3.0 mm. above the base. Styles 1.5–1.9 mm. long, cleft to the base or within 0.3 mm. of the base, attached apically to the nutlets. Nutlets (Figure 10L) black, shiny, smooth, 0.7–0.8 mm. tall, 0.3–0.5 mm. broad, 0.4–0.6 mm. thick dorsi-ventrally, the attachment scar nearly the full length. Chromosome number, not known.

DISTRIBUTION: Limited to two adjacent islands of the Galapagos Archipelago, Bartholomew and James Islands.

Reported flowering times are February and June.

Tiquilia nesiotica has a superficial vegetative resemblance to *T. galapagoa*. It is most easily distinguished from that species by its smooth nutlets which are thicker dorsi-ventrally than broad. It is most closely related to *T. darwinii,* which also has smooth nutlets, and can be distinguished from that species by its larger leaves with spreading, inclined, and appressed hairs; larger corollas without appendages; included stamens; and the nutlets which are deeper dorsi-ventrally than broad.

27. **Tiquilia darwinii** (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Galapagoa darwinii Hooker f., Trans. Linn. Soc. London **20:** 196, 197. 1847. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Chatham Island, Sep. 1835, *C. Darwin s.n.* (Lectotype, CGE, Mus. Henslow!).

Galapagoa fusca Hooker f., Trans. Linn. Soc. London **20:** 197. 1847. TYPE: **Ecuador:** GALAPAGOS ISLANDS. Charles Island, Sep. 1835, *C. Darwin s.n.* (Holotype, CGE, Mus. Henslow!).

Coldenia darwinii (Hooker f.) A. Gray, Proc. Am. Acad. **5:** 340, 341. 1862.

Coldenia fusca (Hooker f.) A. Gray, Proc. Am. Acad. **5:** 341. 1862.

Tiquilia fusca (Hooker f.) A. Richardson, Sida **6:** 236. 1976.

Prostrate, cinereous and brittle, forming mats to 10.0 dm. across; caudices to 11.0 mm. thick; older stems woody with whitish bark; young stems with antrorsely appressed or spreading hairs to 0.6 mm. long. Leaf blades (Figure 8E) obovate to ovate or elliptical, 2.0–2.7 mm. long, 1.2–1.5 mm. broad, marginally entire; upper surfaces with antrorsely appressed fine hairs to 0.2 mm. long and thick bristles to 1.1 mm. long, midrib plicate, lateral veins usually indistinct; lower surfaces more dense with antrorsely inclined hairs, the thickened midrib prominent; petioles trullate, occasionally filiform distally, 1.2–1.5 mm. long, densely ciliate, the abaxial surface

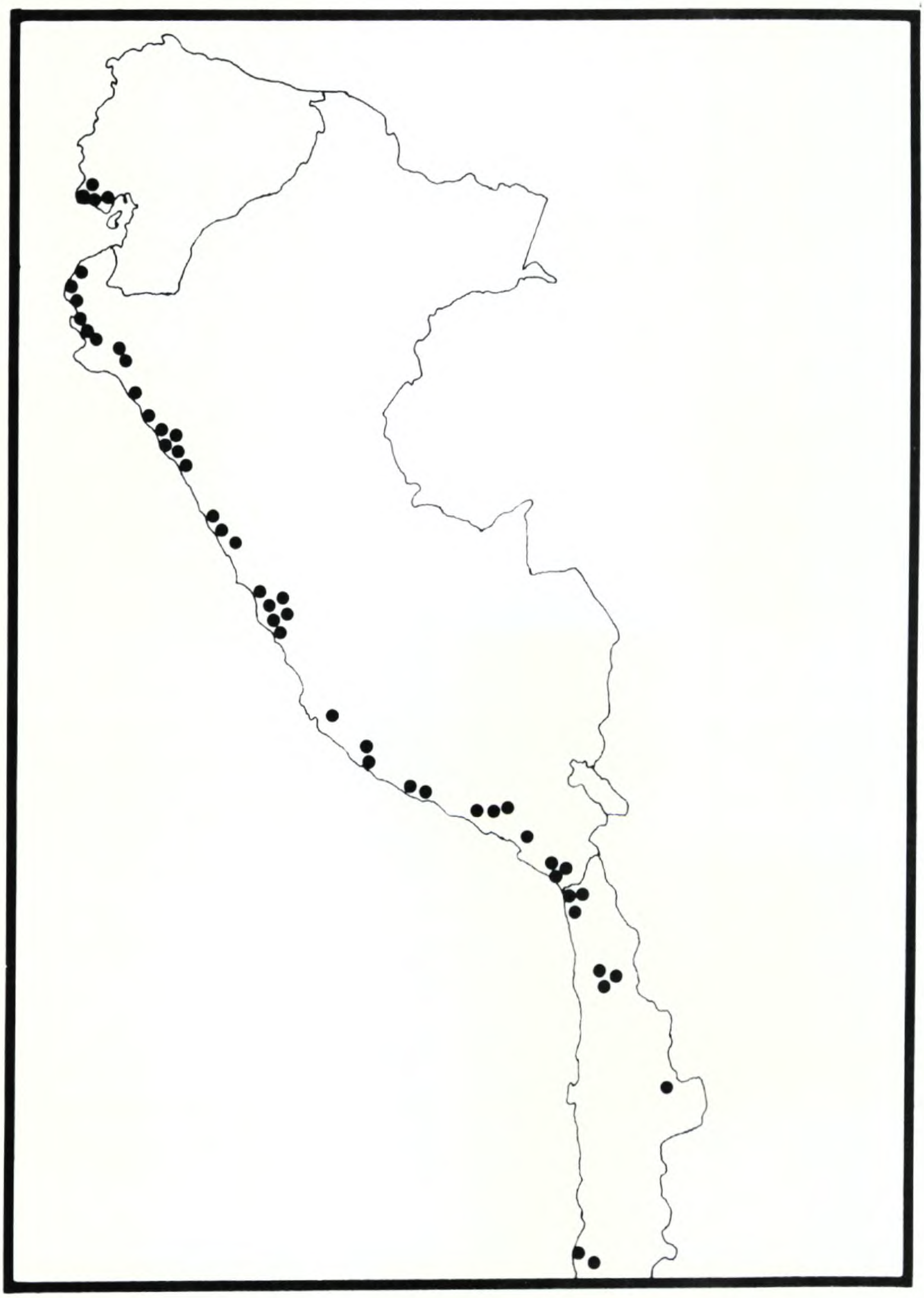

Figure 29. Distribution of *Tiquilia paronychioides*.

with dense antrorsely appressed hairs when young, becoming sparsely pubescent or glabrate. Flowers solitary and axillary, or in small ebracteate groups of 2 or 3 with the leaf clusters. Calyces persistent, 1.4–1.8 mm. long, with fine antrorsely appressed hairs and few stout bristles to 0.3 mm. long, denser distally; lobes 5, subequal, narrowly ovate to subulate, free ca. 1/2 the length; the fused bases usually forming 4 cups enclosing the nutlets. Corollas whitish, 1.3–1.7 mm. long; the buds villous. Stamens extending to the limb or slightly beyond, subequal, adnate equally to the corolla tubes ca. 0.2 mm. above the base, the veins below stamen attachments with small unialate wings. Styles 0.8–1.4 mm. long, cleft to the base or within 0.2 mm. of the base, attached apically to the nutlets. Nutlets (Figure 10M) black, shiny, smooth or minutely granular, 0.6–0.8 mm. tall, 0.3–0.5 mm. broad, the attachment scar nearly the full length, enlarging slightly apically and basally. Chromosome number not known.

DISTRIBUTION: Rather broadly distributed on the Galapagos Islands, on Abingdon, Albemarle, Bartholomew, Blindloe, Charles, Chatham, and James Islands, usually in coastal sands. It is the sole member of the genus on some of the smaller islands but more often shares an island with *T. galapagoa* and/or *T. nesiotica.*

Reported flowering times are February through June, August, and September.

Tiquilia darwinii is most closely related to *T. nesiotica,* both species having smooth, shiny nutlets. It is distinguished from that species by its smaller leaves with all under-surface hairs antrorsely appressed; its smaller, appendaged corollas; and its nutlets with ca. equal dimensions dorsi-ventrally as broad.

EXCLUDED TAXA

Coldenia glabra Phil., Anales Univ. Chile **90:** 229. 1895. TYPE: **Chile:** ATACAMA. Near Caldera, Sep. 1885, *R. Philippi s.n.* (Holotype, SGO!).

Coldenia phaenocarpa Phil., Anales Mus. Nac. Hist. Nat. Chile **2:** 55. 1892. TYPE: **Chile:** TARAPACÁ. Near Calcalhuay, 28 Jan. 1886, *R. Philippi s.n.* (Holotype, SGO!).

Coldenia succulenta Peter, Abh. Königl. Ges. Wiss. Göttingen, Math.-Ph. Kl. **13:** 90. 1928. TYPE: **Tanganyika:** Near Mkomasi, 6 Jun. 1915, *Peter 10857* (Holotype, B!).

= **Heliotropium curassavicum** L., Species Plantarum 130. 1753.

Lithospermum aggregatum Ruiz & Pavon, Prodromus et Flora Peruviana et Chilensis **2:** 4. 1799. TYPE: **Peru:** HUÁNUCO AND JUNÍN. Huánuco and Tarma, not seen. The following herbaria, upon inquiry, reported that the type is not in their possession: BM, F, GH, MA, OXF, and US. The description is too sketchy to evaluate. No species of *Tiquilia* are known from the type locality, which is not typical *Tiquilia* habitat.

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TEXAS SOUTHMOST COLLEGE
BROWNSVILLE
TEXAS 78520

CHROMOSOME STUDIES OF PARNASSIA AND LEPUROPETALON (SAXIFRAGACEAE) FROM THE EASTERN UNITED STATES. A NEW BASE NUMBER FOR PARNASSIA

GERALD J. GASTONY AND DOUGLAS E. SOLTIS

Parnassia is a saxifragaceous genus of approximately 50 species of herbaceous perennials typically found in wet meadows and bogs. The genus ranges throughout the arctic and temperate regions of the northern hemisphere and was recently discussed by Spongberg (1972) as part of a generic flora of the southeastern United States. Spongberg summarized the troubled taxonomic history of *Parnassia,* a genus considered somewhat anomalous in the Saxifragaceae, but focused most of his discussion on the taxonomic position and interspecific relationships of four species which occur in the eastern United States. These species, *P. asarifolia, P. grandifolia, P. caroliniana,* and *P. glauca,* all belong to sect. *Parnassia* and, with the exception of *P. glauca,* they are all local or rare. Spongberg noted that considerable taxonomic confusion has resulted from the morphological similarities among *P. grandifolia, P. caroliniana,* and *P. glauca,* and he summarized the characters by which they can be distinguished. In addition, we have found in our material that *P. caroliniana* possesses a long creeping rhizome which contrasts sharply with the short erect rhizomes of *P. grandifolia* and *P. glauca.*

Spongberg reported that a chromosome base number of $x = 9$ characterizes *Parnassia,* but noted that none of the species of this eastern United States complex has been examined cytologically. A base number of $x = 8$ has been indicated by the reported count of $2n = 16$ for Himalayan *P. nubicola* of sect. *Nectarotribolos* as cited by Federov (1969). This anomalous base number led us to investigate the original source of the *P. nubicola* count, and this search has revealed several errors in the literature that we correct here in collaboration with Dr. J. L. Hamel.

The source of the reference to $2n = 16$ for *Parnassia nubicola* from Bhutan is a paper by Hamel (1953). Reference works by Chadefaud and Emberger (1960) and Federov (1969) in which numbers based on $x = 8$ are reported for *Parnassia* species have apparently taken their data from Hamel's table (1953, p. 266) in

which these numbers are simply typographical errors (Hamel, pers. comm.). Earlier in his paper (fig. 88 and pp. 225–228), Hamel clearly indicated that in *P. nubicola* $2n = 18$. He also correctly attributed counts based on $x = 9$ to the other *Parnassia* taxa which are erroneously recorded in his table as based on $x = 8$. Hamel (pers. comm.) shares our view that the counts of $2n = 20$ by Pace (1912; see also Hamel, 1953, p. 226) and by Tischler (1934) in *P. palustris* may actually be misinterpretations of $2n = 18$. Prior to our report, therefore, the only accurately recorded and undisputed base number in *Parnassia* is $x = 9$, with diploids, triploids, tetraploids, and hexaploids known.

Spongberg (1972) also discussed the monotypic genus *Lepuropetalon,* which is known disjunctively from the southeastern United States and Mexico, central Chile, and Uruguay and which is thought to be closely related to *Parnassia* on the basis of similarities in floral and tannin sac morphology. He suggested that a chromosome count from this cytologically unknown genus might further substantiate this relationship, as recent palynological data have done (Hideux & Ferguson, 1976).

In an effort to determine whether cytotaxonomic differences exist within this *Parnassia* complex and to provide new data pertaining to the putative relationship between *Parnassia* and *Lepuropetalon,* we have undertaken a cytological examination of these *Parnassia* species and *L. spathulatum*.

MATERIALS AND METHODS

Root tips for mitotic squashes were obtained from the following sources. Living plants of *Parnassia* species were collected in the field (Table 1) and subsequently cultured in the Indiana University greenhouses. Plants of *Lepuropetalon spathulatum* were grown from seed obtained from herbarium specimens (*Thomas 43386* & *43527* NLU; Table 1) and were cultured on a sand-soil mixture in the laboratory.

Mitotic squashes were based on the technique of Roy and Manton (1965) except that in view of the small size of the chromosomes, the paradichlorobenzene treatment was omitted and the snail cellulase ("glusulase") was obtained in prepared form from Endo Laboratories, Inc., Garden City, N. Y. Slides were made permanent in Permount following the method of Sears

(1941). A single chromosome squash is illustrated for each species, but at least three replicate counts of each have substantiated the illustrated numbers. Vouchers are cited in the captions of figures. Photographs for Figures 1, 5, and 9 utilized phase contrast optics; those for Figures 3 and 8 used bright field.

Table 1. **Collections Studied.**

Parnassia asarifolia Vent. **Virginia,** BLAND CO.: along both margins of Dismal Creek, 0.6 mi. NE of jct. of Appalachian Trail with Rte. 606, 0.1 mi. from Giles Co. line. *Soltis 971.*

Parnassia grandifolia DC. **North Carolina,** ASHE CO.: bog, bordering unmarked dirt road on E slope of Bluff Mt., ca. 2.5 mi. NW of Beaver Creek Church. *Soltis 970.*

Parnassia caroliniana Michx. **North Carolina,** LEE CO.: overgrown ditch near margin of wooded area along RR right-of-way, 0.3 mi. E of jct. of Rtes. 1176 & 1179. *Soltis 1008.*

Parnassia glauca Raf. **Indiana,** TIPPECANOE CO.: Flint Creek Hill Marsh, bordering Reserve Rd., 0.1 mi. from Fountain Co., 2.5 mi. W of West Point. *Soltis 969.*

Lepuropetalon spathulatum (Muhl.) Ell. **Louisiana,** BIENVILLE PARISH: under edge of building of Mt. Olive Baptist Church beside La. 147 jct. with La. 155, Sec. 32, T16N, R4W. *Thomas 43386* NLU. **Louisiana,** CADDO PARISH: cemetery and road bank of Fluornoy-Lucas Rd. at jct. with U.S. 171, Shreveport. *Thomas 43527* NLU.

RESULTS AND DISCUSSION

The mitotic chromosome squashes reported here (Figures 1–10) provide the first counts for *Parnassia asarifolia, P. grandifolia, P. caroliniana, P. glauca,* and *Lepuropetalon spathulatum.* The number for all four *Parnassia* species is $2n = 32$, whereas that for *L. spathulatum* is $2n = 46$.

Our counts of *Parnassia,* all based on $x = 8$, indicate that these species are tetraploid and establish a new base number for the genus. All previous known counts of *Parnassia* species have been summarized in Federov (1969). Several of these taxa have been

subsequently recounted, but without the addition of any new numbers (Ornduff, 1967, 1968; Moore, 1973). The counts of $2n = 16$ (*P. nubicola* and *P. palustris*) and $2n = 32$ (*P. obtusiflora*) given by Hamel (1953, p. 266) and repeated in part by Chadefaud and Emberger (1960) and Federov (1969) are erroneous, as discussed above. The cytological data presented here complement previous morphological data in delimiting these four eastern United States species of *Parnassia* as a natural group.

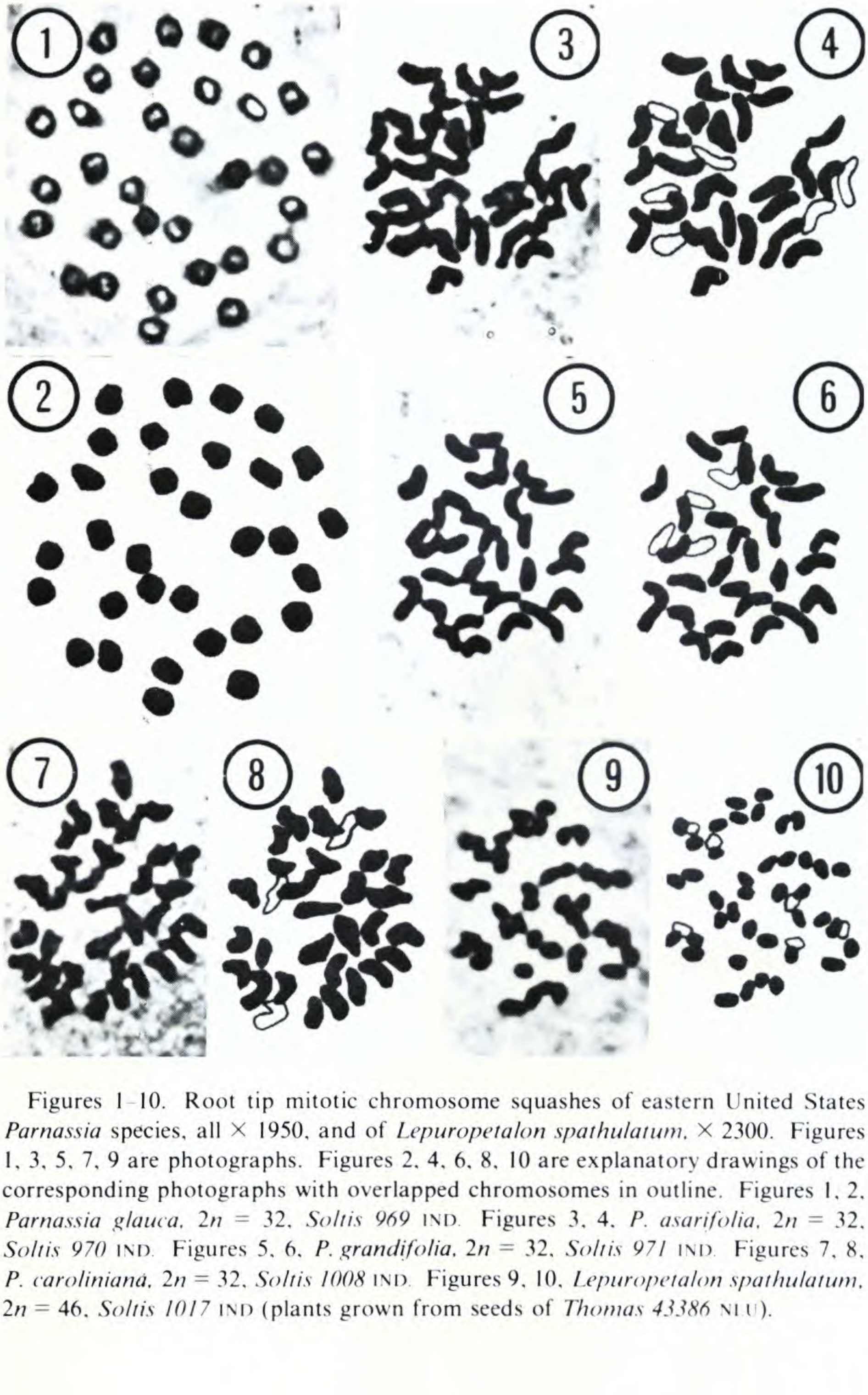
Our counts of $2n = 46$ for *Lepuropetalon spathulatum* provide the first chromosome data for this genus whose taxonomic history has been summarized by Spongberg (1972). Based on the data in Federov (1969), this number is uncommon in the Saxifragaceae, known only as part of the aneuploid series in *Saxifraga granulata* and *S. sp.* (*moschata* or *exarata*?). This high chromosome number does not readily support the putative relationship between *Lepuropetalon* and *Parnassia*. In fact, it does little to support the inclusion of *Lepuropetalon* in the Saxifragaceae. It could have been variously derived, for example via an aneuploid decrease from $2n = 48$. Only through such a hypothetical permutation would *Lepuropetalon* relate cytologically to *Parnassia* by sharing the herein established base number of $x = 8$. Counts of *Lepuropetalon* from its other disjunct stations may be instructive in this regard.

SUMMARY

A cytological study of four species of *Parnassia* from the eastern United States has firmly established a new base number ($x = 8$) for the genus and has corrected previous erroneous references to a base number of $x = 8$ for other species in the genus. *Lepuropetalon* has been considered closely related to *Parnassia* based on morphological similarities. New evidence from cytology presented here can be variously interpreted but does not readily support the proposed close affinity between the two genera.

ACKNOWLEDGMENTS

We are grateful to Dr. J. L. Hamel, Samoëns, France, for confirming our interpretation of the cited table in his 1953 paper. We thank Dr. R. Dale Thomas for supplying material of *Lepuropetalon* and Dr. C. H. Haufler and Georgia Soltis for technical assistance and advice.



Figures 1–10. Root tip mitotic chromosome squashes of eastern United States *Parnassia* species, all × 1950, and of *Lepuropetalon spathulatum*, × 2300. Figures 1, 3, 5, 7, 9 are photographs. Figures 2, 4, 6, 8, 10 are explanatory drawings of the corresponding photographs with overlapped chromosomes in outline. Figures 1, 2, *Parnassia glauca*, $2n = 32$, *Soltis 969* IND. Figures 3, 4, *P. asarifolia*, $2n = 32$, *Soltis 970* IND. Figures 5, 6, *P. grandifolia*, $2n = 32$, *Soltis 971* IND. Figures 7, 8, *P. caroliniana*, $2n = 32$, *Soltis 1008* IND. Figures 9, 10, *Lepuropetalon spathulatum*, $2n = 46$, *Soltis 1017* IND (plants grown from seeds of *Thomas 43386* NLU).

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DEPARTMENT OF BIOLOGY
INDIANA UNIVERSITY
BLOOMINGTON, INDIANA 47401

ADDITIONAL NOTES ON VERONICA ANAGALLIS-AQUATICA × CATENATA (SCROPHULARIACEAE)

LAWRENCE HECKARD AND PETER RUBTZOFF

Brooks (1976) reports and describes a sterile putative hybrid between *Veronica anagallis-aquatica* L. and *V. catenata* Pennell that was found growing with the presumed parents in central and western Nebraska. We would like to report the occurrence of this same hybrid in California and add information from the literature on studies of this hybrid in Europe.

There has been considerable confusion in the nomenclature of *Veronica catenata* that apparently hinders the dissemination of information on this species. In current major regional floras of the United States this species can be found under the names *V. catenata, V. comosa* Richter, *V. connata* Raf., and *V. salina* Schur., and much published work on the species in Europe, including studies on hybridization, is under *V. aquatica* Bernh. Burnett (1950) reviewed the nomenclatural history of this species and gave arguments for accepting *V. catenata* as the correct name. Much of the early work on *V. anagallis-aquatica* appears under the shortened name *V. anagallis* L. Omitted from Brooks' paper was a consideration of the wide distribution of both parental species in Eurasia in addition to North America (Pennell, 1935; Fernald, 1939; Hartl, 1968).

While Brooks' report is the first of which we are aware for the hybrid in North America, the author failed to mention that this hybrid, as pointed out in *Flora Europaea* (Walters & Webb, 1972) and other British and continental floras (e.g., Hartl, 1968), is well-known throughout much of Europe, sometimes forming large clones in streams. Our earliest reference to the hybrid goes back to Lackschewitz (1908), who described the intermediate-appearing hybrids in Latvia and illustrated the parents and hybrid with its aborted pollen grains. A name honoring Lackschewitz was given to the hybrid by Keller (1942): *Veronica* × *lackschewitzii.* Schlenker (1936) carried out an extensive program of artificial hybridization between the two species which resulted in numerous, mostly sterile F_1 plants and 33 morphologically diverse F_2 plants, of which one was selfed to produce F_3 plants that displayed considerable varia-

tion in fertility. Davis and Heywood (1963) point out that while *V. anagallis-aquatica* and *V. catenata* intergrade in continental Europe, they form sterile hybrids and remain separable in Great Britain, a situation which they attribute to differences in selection pressure, the hybrids having an advantage in one area and not in the other. Experimental work has been done recently in Great Britain by Marchant (1970) and some of his results are briefly summarized by Walters (1975).

In California, where it seems likely that both species are introduced, we have found hybridization between *Veronica anagallis-aquatica* and *V. catenata.* These species are spreading in California and the chances for their sympatric occurrences are increasing. We have found mixed populations of the two species in four localities in central and northern California, and hybrids occurred in one of these colonies: Siskiyou County: Shasta River, highway 99 bridge ca. 5 miles north of Yreka, 28 Aug. 1971 (*Heckard 2783,* JEPS). The hybrids displayed complete seed sterility and 97% of the pollen grains were aborted and non-staining (in lacto-phenol and cotton blue). Examination of microspore formation showed clusters of five to ten microspores of varying sizes indicating the occurrence of considerable meiotic irregularity. Pollen in the parents showed an insignificant 3–8% of aborted grains. Dr. Tsan-Iang Chuang has kindly supplied us with chromosome counts for both parents at the same locality as the hybrid. Both *V. anagallis-aquatica* (*Heckard 2781,* JEPS) and *V. catenata* (*Heckard 2782,* JEPS) have 18 pairs ($2n = 36$), which agrees with counts for these species in Europe. The few hybrid plants along the Shasta River grew intermingled with the two parental species at the edge of pools in the drying sand of the river margin. For the most part the morphological features of the hybrids and parental species are in agreement with those described by Brooks. Although Brooks used plant height as a distinguishing feature for the two parental species, we find that in California the variation in height is so great for each species that it would seem unsuitable for separating them. In fact, at the Shasta River locality, *V. catenata* happened to be taller, which conflicts with the Brooks data. One additional feature noted in the Shasta River hybrid was the size of corolla: 5–6 mm. broad which is intermediate between that of *V. anagallis-aquatica* (6–7 mm.) and *V. catenata* (4–5 mm.). Corolla color is the most useful feature for distinguishing the two parental species in the field: light

blue in *V. anagallis-aquatica* and pale pink in *V. catenata.* We did not get a record of flower color in the hybrid. Schlenker (1936) shows (in a colored plate) the corolla of the artificial hybrid to be similar in color and size to that of *V. anagallis-aquatica.*

Brooks' statement that natural hybrids in Scrophulariaceae are infrequent may be misleading. In *Veronica,* for which no hybrids were known by Brooks, we are aware of three instances of hybridization in Europe, involving six species other than *V. anagallis-aquatica* and *V. catenata* (Beatus, 1936; Hartl, 1968; Walters & Webb, 1972). Also, Hultén (1937) reports suspected hybridization between *V. stelleri* Pall. ex Spreng. and *V. wormskjoldii* Roem. & Schult. in the Aleutian Islands. Hybrids are commonly encountered in such North American genera as *Mimulus, Orthocarpus, Penstemon,* and *Castilleja,* the latter being notably promiscuous. In Europe, *Euphrasia* is equally promiscuous and hybrids are common in *Antirrhinum* and *Verbascum.* Thus natural hybrids are perhaps more frequent and certainly no more infrequent in Scrophulariaceae than in most other families of similar size.

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JEPSON HERBARIUM, BOTANY DEPARTMENT
UNIVERSITY OF CALIFORNIA
BERKELEY, CA. 94720

A NEW COMBINATION IN GRINDELIA (COMPOSITAE-ASTEREAE)

JOHN RUFFIN

Xanthocephalum gymnospermoides (Gray) Benth. & Hook. is a stout, annual, fall-blooming species known from central Mexico (Solbrig, 1960) extending into the mountains of Southern Arizona and New Mexico. It is characterized by the brownish-green bark of the stem. The leaves are of variable sizes and are quite glutinous with entire, toothed or slightly serrated margins. Heads, containing a large number of ray and disc florets, are numerous and crowded at the end of the branchlets. The involucre is campanulate and glutinous, while the pappus is variable and may appear as a low crown or as several irregularly shaped awns.

Since its original description (as a *Gutierrezia*) by Asa Gray in 1853, the identity of *Xanthocephalum gymnospermoides* has been a source of confusion and its generic affinity has not been satisfactorily ascertained. This species has been previously referred to as *Gutierrezia gymnospermoides* by Gray in 1853; *Guenthera viscosa* by Regel in 1858; and *Grindeliopsis gymnospermoides* (Gray) Sch. Bip. in 1858.

Asa Gray (1873) emphasized the close similarity between *Xanthocephalum* and *Gutierrezia* and chose to accept Bentham and Hooker's revision of transferring *X. gymnospermoides* to the genus *Gutierrezia.* However, Gray indicated the relationship was still not perfectly clear.

In his documentation of the species, Regel indicated that this species definitely does not belong to the genus *Gutierrezia,* has the character of a *Grindelia,* and also shows relationships with *Heterotheca, Bradburia* and *Dieteria.*

More recently the closeness of *Xanthocephalum gymnospermoides* to *Grindelia* has been expressed by Solbrig (1960), who emphasized the similarities of the involucre, habit and chromosome numbers.

I have noticed during a study of the morphology and anatomy of this genus that *Xanthocephalum gymnospermoides* differs in many respects from other species in the *Xanthocephalum* complex (Ruffin, 1974a) and have questioned the proposed relationships. In addition to certain general characteristics such as the type of

pappus, shape of the involucre, and the resinous character of the involucre and leaves, which suggest an affinity with the genus *Grindelia*, there are several more specific similarities which appear to suggest that *Xanthocephalum gymnospermoides* should indeed be transferred into the genus *Grindelia*.

Koch (1930) described the floral anatomy of *Grindelia squarrosa*. The reduction in the number of vascular strands at the base of the florets and the separation of the bundles at the top of the achene of *G. squarrosa* are representative of the condition noted in *Xanthocephalum gymnospermoides* (Ruffin, 1974a). The highly reduced vasculature in the achene of several other species of *Grindelia* has also been reported by Anderson and Weberg (1974). The supply to the achene divides into two strands. At the top of the ovary the two bundles that have persisted through the ovary wall separate into five bundles which lead into the corolla. Bundle numbers in the ovary of the other species of *Xanthocephalum* were more commonly five, less frequently ten.

The large vessel elements and libriform fibers as well as other xylary feature of *Grindelia decumbens*, *G. squarrosa* and *G. squarrosa* var. *nuda* as described by Anderson and Weberg (1974) reflect similar conditions noted for *Xanthocephalum gymnospermoides* (Ruffin, 1974b). Despite the somewhat larger vessel and libriform fiber elements, the xylary features of *X. gymnospermoides* certainly seem to express a closer affinity with the species of *Grindelia* than with other species of *Xanthocephalum*.

In addition to having features of habit, morphology and anatomy similar to those of *Grindelia*, *Xanthocephalum gymnospermoides* is chromosomally indistinguishable from *Grindelia* with $n = 6$ (DeJong & Longpre, 1963; Raven et al., 1960; Solbrig, 1960; Turner et al., 1962). The cytological condition of all the other *Xanthocephalum* species studied shows a base chromosome number of four.

The features of *Xanthocephalum gymnospermoides* which set it apart from the other species of *Xanthocephalum* appear to be conclusive evidence that *X. gymnospermoides* should be referred to the genus *Grindelia*.

Grindelia gymnospermoides (A. Gray) Ruffin, comb. nov.

Gutierrezia gymnospermoides A. Gray, Plantae Wrightianae **2:** 79. 1853.

Guenthera viscosa Regel, Gartenflora **7:** 44. 1858.

Grindeliopsis gymnospermoides (A. Gray) Sch. Bip. Bonplandia **6:** 356. 1858 (nomen nudum).

Xanthocephalum gymnospermoides (Gray) Benth. & Hook. f. Gen Pl. **2:** 249. 1873.

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GRAY HERBARIUM
HARVARD UNIVERSITY
22 DIVINITY AVENUE
CAMBRIDGE, MASSACHUSETTS 02138

Rhodora

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INDEX TO VOLUME 79

New scientific names are printed in **bold face**

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N.E.Botanical Club,Inc.,Botanical Museum, Harvard University,Oxford Street,Cambridge,MA 02138

EDITOR *(Name and Address)*
Prof. Rolla M. Tryon, 22 Divinity Ave.,Cambridge,Mass.02138

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Mrs. Harmony Spongberg, 22 Divinity Ave., Cambridge,Mass. 02138

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RHODORA October, 1977 Vol. 79, No. 820

CONTENTS